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Classification, phylogeny and zoogeography of the North American species of *Siphona* Meigen (Diptera, Tachinidae)

by

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SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Classification, phylogeny and zoogeography of the North American species of Siphona Meigen (Diptera, Tachinidae) submitted by James E. O'Hara in partial fulfilment of the requirements for the degree of Master of Science.

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Date.. October 2, 1981

ABSTRACT

Members of the cosmopolitan genus *Siphona* are small tachinid flies with a long geniculate proboscis. Their known hosts are *Tipula* spp. (Tipulidae) and Microlepidoptera (especially Noctuidae).

Siphonopsis Townsend, with the following three species, is removed from synonymy with *Siphona*, type-species *Siphonopsis plusiae* (Coquillett) (California), *Siphonopsis brasiliensis* Townsend (Brazil) and *Siphonopsis conata* Reinhard (California). Two species, *Crocuta alticola* Mesnil (Burma) and *Crocuta crassulata* Mesnil (Burma), are placed in *Ceranthia s. lat*. *Siphona diluta* van der Wulp (Mexico) is transferred to *Clausicella*. *Crocuta malaisei* Mesnil (Burma) and *Crocuta pellex* Mesnil (Burma) are placed in *Actia*. *Phantasiosiphona* Townsend is synonymized with *Siphona*, with type-species *P. tropica* Townsend (Mexico) and *P. kuscheli* Cortés (Juan Fernández Islands).

Twenty-one *Siphona* species of North America (America north of Panamá-Colombia border) are recognized and described, including 11 new species. Three species described from the Palearctic Region represent new New World records: *S. cristata* (Fabr.), *S. hokkaidensis* Mesnil and *S. maculata* Staeger. A species described from western United States, *S. lurida* Reinhard, is a new Palearctic record (from Japan). Two keys are provided for identification of adult specimens, one to species of America north of Mexico and the other to Middle American species. Male and female head profiles and male genitalia are illustrated for all species. Known distributions of North American species are mapped.

Six species groups are recognized in North America on the basis of a cladistic analysis of 15 characters of adults. A cladogram is presented for each species group, showing hypothetical phylogenetic relationships among North American species. The *S. maculata* group is inferred to be the most primitive of the North American species groups. Available data are insufficient to determine phylogenetic relationships among the other species groups. Analysis of Palearctic *Siphona* species illustrate the general applicability of North American species groups to species in other regions.

The following six species groups with their included species are: (1) *S. maculata* group: *S. floridensis* n.sp. (type-locality Orlando, FA), *S. intrudens* (Curran), *S. lurida* Reinhard, *S. maculata* Staeger and *S. pacifica* n.sp. (type-locality Dartford, WA), (2) *S. cristata* group: *S. cristata* (Fabr.), *S. lutea* (Townsend), *S. multifaria* n.sp. (type-locality mi. 87, Dempster Hwy., Y.T.), *S. oligomyia* n.sp. (type-locality Keremeos, B.C.) and *S. pisinnia* n.sp. (type-locality 21km. n. Silver City, NM), (3) *S. geniculata* group: *S. hokkaidensis* Mesnil, *S. geniculata* (De Geer) and *S. medialis* n.sp. (type-locality Lockeport, N.S.), (4) *S. futilis* group: *S. brunnea* n.sp. (type-locality Zontehuitz, Chiapas, Mex.), *S. futilis* Wulp and *S. illinoiensis* Townsend, (5) *S. tropica* group: *S. akidnomyia* n.sp.

(type-locality Zontehuitz, Chiapas, Mex.), *S. longissima* n.sp. (type-locality 10mi. ne. San Cristobal de las Casas, Chiapas, Mex.), *S. rizaba* n.sp. (type-locality Orizaba, Veracruz, Mex.), and *S. tropica* (Townsend), and (6) *S. macronyx* group: *S. macronyx* n.sp. (type-locality Pullman, WA).

S. tenuis Curran is synonymized with *S. lutea* (Townsend), *S. ceres* (Curran) with *S. futilis* Wulp and *S. silvarum* Herting with *S. hokkaidensis* Mesnil. Lectotypes are designated for *S. futilis* Wulp, *S. illinoiensis* Townsend and *S. lutea* (Townsend).

Three general distribution patterns are evident within species groups of *Siphona* (1) America north of Mexico and the Palearctic Region - *S. maculata*, *S. cristata* and *S. geniculata* groups, (2) America north of Mexico and Middle America - *S. futilis* group, and (3) Middle America and Afrotropical Region - *S. tropica* group. Within North America, distribution patterns of *Siphona* species are classed as follows: (1) transcontinental - *S. cristata*, *S. hokkaidensis*, *S. intrudens*, *S. lutea*, *S. maculata*, *S. medialis* and *S. multifaria*, (2) western - *S. geniculata* (introduced), *S. lurida*, *S. macronyx*, *S. oligomyia*, *S. pacifica* and *S. pisinnia*, and (3) Mexican - *S. akidnomyia*, *S. brunnea*, *S. futilis*, *S. longissima*, *S. rizaba* and *S. tropica*.

A historical zoogeographic analysis seeks an explanation to these distribution patterns. The patterns are

considered in the context of current paleoclimatic and paleogeographic hypotheses to arrive at several conclusions about the historical zoogeography of *Siphona* species: (1) *Siphona* is hypothesized to have originated in Africa between the Late Cretaceous and Early Oligocene, (2) a *S. tropica* group taxon was first to enter the New World, following a northern paratropical route between Eurasia and North America, no later than the Early Oligocene, (3) the first taxa of the *S. cristata*, *S. geniculata* and *S. maculata* groups migrated to North America through Beringia after the Tertiary climatic optimum, probably no earlier than Late Miocene, (4) exchange between Old and New World's continued within the *S. cristata*, *S. geniculata* and *S. maculata* groups into the Pleistocene, and (5) three species pairs represent Pleistocene vicariant events: *S. maculata* and *S. floridensis*, *S. lutea* and *S. oligomyia*, and *S. futilis* and *S. illinoiensis*.

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My wife, Wendy, assisted in many ways. As a companion on field trips, she helped collect tachinid specimens. She also prepared locality data lists and distribution maps, and typed portions of the manuscript into the computer.

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1. INTRODUCTION

Specimens of *Siphona* species are small (3-6mm long) tachinids of cosmopolitan distribution. Like most other tachinids, they spend their three larval instars as internal parasitoids of other insects. Chiefly parasitic on larval Microlepidoptera in general and the Noctuidae in particular (if the meagre data available are any indication), a few species parasitize their distant dipteran relatives, *Tipula* species (Tipulidae).

As parasitoids of other insects, tachinids are highly regarded for their role in the natural environment and their potential for use as control agents against pest insects. When the introduced pest *Tipula paludosa* Meigen began damaging lawns and meadows in parts of Newfoundland, Cape Breton Island and the lower Fraser Valley of British Columbia, a Palearctic parasitoid was sought for its control. *Siphona geniculata* (De Geer) was recommended for introduction and became part of a biological control program on both coasts (Wilkinson, 1971). Though little success has been achieved in limiting *T. paludosa* populations by *S. geniculata* (Wilkinson, per. comm.), the program illustrates the desirability of an alternative to long term chemical control of a pest species.

Whether New World *Siphona* species are economically important, or have the potential to be so, is unknown. Until now even taxonomic aspects have been neglected, so a framework has not been developed upon which to build a more comprehensive knowledge of the group. This paper represents a step in that direction by providing a revision to North American[1] *Siphona* species.

The history of North American *Siphona* classification has been primarily one of individual species descriptions under varied generic names. Curran (1932) tried to improve the situation through publication of a key to North American *Siphona* species, but evidently based the key mainly on descriptions. As a result, an assemblage of species belonging to three genera were keyed according to untrustworthy and insignificant characteristics. Furthermore, two described *Siphona* species were apparently overlooked, for they were not treated in the key.

Judged from a historical perspective, the list of eight *Siphona* species compiled by Sabrosky and Arnaud (1965) represented a significant contribution. It was from this source that my first impression of the number of species and constitution of the genus in the Nearctic Region was gleaned.

Once embarked on a revision of Nearctic *Siphona* species, I was soon to discover the inadequate state of the classification - a result of lack of attention, not expertise. Entwined with species problems was the more basic question of how to define the genus. In answering this question my area of coverage was extended to include Middle America, for it was chiefly through study of *Siphonopsis* species and allied genera from southwestern United States and Mexico that I recognized the fundamental difference between those taxa and *Siphona*.

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[1] America north of Panamá-Colombia border

A major part of this paper is concerned with classificatory aspects of North American *Siphona* species. Also considered are phylogenetic and zoogeographic aspects, with reference to species from other regions. Due to the excellent taxonomic contributions of Dr. L.P. Mesnil (1960, 1961, 1964 and 1965), it has been possible to study interrelationships between North American (particularly Nearctic) and Palearctic *Siphona* species.

Species groups are recognized for the first time in *Siphona*. Based on cladistic relationships it is hoped these will have general applicability.

2. MATERIALS AND METHODS

2.1 Materials

This study was based on examination of approximately 4000 adult specimens of *Siphona* and related siphonines, borrowed from the following institutions and individuals. Abbreviations are those used in the text to indicate deposition of specimens.

2.1.1 Institutional loans

AMNH Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024; P. Wygodzinsky.

BMNH Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD; J.P. Dear.

CAES Connecticut Agricultural Experiment Station, 123 Huntington Street, Box 1106, New Haven, CT 06504; K.A. Welch.

CAS Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118; P.H. Arnaud, Jr.

CNC	Biosystematics Research Institute, Central Experimental Farm, K.W. Neatby Building, Ottawa, Ontario K1A 0C6; D.M. Wood.
CSU	Department of Zoology and Entomology, Colorado State University, Fort Collins, CO 80523; H.E. Evans.
CUI	Department of Entomology, Cornell University, Comstock Hall, Ithaca, NY 14853; L.L. Pechuman.
FSCA	Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Gainesville, FL 32602; H.V. Weems, Jr.
INHS	Illinois Institute of Natural Resources, Section of Faunistic Surveys and Insect Identification, Illinois Natural History Survey, 172 Natural Resources Building, Urbana, IL 61801; D.W. Webb.
KSU	Department of Entomology, Kansas State University, Waters Hall, Manhattan, KS 66506; H.D. Blocker.
KUR	Biological Laboratory, College of General Education, Kyushu University, Ropponmatsu, Fukuoka 810, Japan; H. Shima.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138; M.K. Thayer.

MSU	Department of Entomology, Michigan State University, East Lansing, MI 48824; R.L. Fischer.
MSUB	Department of Biology, Montana State University, Bozeman, MT 59717; S. Rose.
NCSU	Department of Entomology, Entomology Museum, North Carolina State University, Box 5215, Raleigh, NC 27650; C.S. Parron.
NDSU	Department of Entomology, North Dakota State University, Fargo, ND 58102; E.U. Balsbaugh, Jr.
NSM	Nova Scotia Museum, 1747 Summer Street, Halifax, Nova Scotia, B3H 3A6; B. Wright.
OKSU	Department of Entomology, Oklahoma State University, 501 Life Sciences West, Stillwater, OK 74074; W.A. Drew.
OSU	Department of Entomology, Oregon State University, Corvallis, OR 97331; M.D. Schwartz.
OUCO	Department of Entomology, Ohio State University, 103 Botany and Zoology Building, 1735 Neil Avenue, Columbus, OH 43210; C.A. Triplehorn.

PSU	Frost Entomological Museum, Department of Entomology, Pennsylvania State University, University Park, PA 16802; S.W. Frost.
ROM	Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6; G.B. Wiggins.
SMNS	Staatl. Museum für Naturkunde, Stuttgart, D-714 Ludwigsburg, Arsenalplatz 3, West Germany; B. Herting.
UAF	Department of Entomology, University of Arkansas, Fayetteville, AR 72701; R. Chenowith.
UASM	Department of Entomology, Strickland Museum, University of Alberta, Edmonton, Alberta T6G 2E3; G.E. Ball.
UCD	Department of Entomology, University of California, Davis, CA 95616; R.O. Schuster.
UCR	Department of Entomology, University of California, Riverside, CA 92521; S.I. Frommer.
UCS	Facultad de Agronomía, Universidad de Chile, Casilla 1004, Santiago, Chile; R. Cortés.
UGA	Department of Entomology, University of Georgia, Athens, GA 30602; C.L. Smith.

UGG	Department of Environmental Biology, University of Guelph, Guelph, Ontario N1G 2W1; S. Marshall.
UKL	Department of Entomology, Snow Entomology Museum, University of Kansas, Lawrence, KS 66045; C.D. Michener and G.W. Byers.
UMW	Department of Entomology, University of Manitoba, Winnipeg, Manitoba R3T 2N2; T.D. Galloway.
USNM	Systematic Entomology Laboratory, SEA, U.S. Department of Agriculture, United States National Museum, Washington, DC 20560; C.W. Sabrosky.
USP	Museu de Zoologia, Universidad de São Paulo, Avenida Nazare, 481, Caixa Postal 7172, 04263, São Paulo, sp, Brazil; J.H. Guimarães.
WSUP	Department of Entomology, James Entomological Collection, Washington State University, Pullman, WA 99164; Curator.

2.1.2 Loans from private collections

DMW	D.M. Wood, see CNC.
WLD	W.L. Downes, c/o P.L. Fischer, MSU.

JEOH designates specimens in my personal collection.

2.2 Methods

2.2.1 Criteria for ranking of taxa

My concept of a bisexual species is essentially that of Mayr (1969: 26), whereby reproductive isolation of populations is the basic criterion upon which the concept is based. Seldom is it practical, or even possible, for a systematist to field test this hypothesis with phena under revision. Rather, reproductive isolation is inferred from other data.

I used two criteria to aid in recognition of species. One was distributional data and the other phenetic divergence.

Widely sympatric phena were assumed to represent species, for otherwise interbreeding would presumably have led to deterioration of phenetic difference (barring ecological or temporal barriers). For phenetically similar species like *S. cristata* and *S. multifaria*, and *S. maculata* and *S. intrudens*, this criterion was especially useful.

The degree of phenetic divergence exhibited among sympatric species provided an indication of interspecific variation within *Siphona*. Along with studies of intraspecific variation, it became possible to distinguish which allopatric phena were sufficiently unique phenetically as to represent species.

The subspecific category (as discussed by Mayr, 1969: 187-197) has not been used in this work. It was considered for the polymorphic population of *S. hokkaidensis*, but rejected as inappropriate for reasons given under "Variation" of that species. Geographical distributions and structural characteristics of other phena were such that the subspecific category was not a viable alternative.

Species sharing one or more derived states and representing apparently monophyletic lineages were arranged under the informal category of species groups.

2.2.2 Specimen examination

Pinned, dried specimens were examined with a Wild M5 stereoscopic microscope with standard light source, at magnifications up to 50X. Genitalia were studied with a Leitz SM-LUX compound microscope at magnifications up to 400X.

2.2.3 Measurements

Body length was measured dorsally at 50X through a Wild M5 stereoscopic microscope with an ocular micrometer (100 divisions) calibrated to a slide micrometer (100 divisions to the millimeter). Body length was taken as length from pedicel to scutellum plus abdominal length from attachment to thorax to apex of tergum 5. This measurement eliminated differences due to position of antennae and abdomen relative to rest of body.

Head measurements of eye and head height and length of flagellomere 1 were taken in profile, as shown in Fig. 1.

Proboscis length was taken as combined length of prementum and labella. Prementum was measured basally from ventral edge of sclerotization to most distal point. Labellar length was measured from dorsal base of labella to labellar tip. Head measurements were taken at 50X with an ocular micrometer, and expressed in text and Hubbs-Hubbs diagrams in ratios.

Illustrations are provided with indicators to actual size. These were obtained by projecting an image of a slide micrometer through a camera lucida (see "Illustrations" below) onto the drawing.

2.2.4 Hubbs-Hubbs diagrams

Hubbs-Hubbs diagrams representing intraspecific variation in height of compound eye, lengths of flagellomere 1 and proboscis (Figs. 13-15), and ratio length of flagellomere 1: eye height (Fig. 16) were prepared. Male specimens were chosen for representation in Hubbs-Hubbs diagrams because their eye and flagellomere 1 display greater interspecific differences than females. Proboscis length is not sexually dimorphic so measurements from female specimens were included in Fig. 15 for species with few male specimens.

Hubbs-Hubbs diagrams are arranged as follows. Species names are along the left margin, abbreviated to their first four letters and listed in order of proboscis length, from shortest to longest. *S. hokkaidensis* is divided into samples "a" and "b", as discussed under variation of that species. Number of specimens measured is given along the right margin. The appropriate ratio is along the X-axis.

2.2.5 Illustrations

All illustrations were made with the aid of a camera lucida, as detailed below, and later inked to mylar drafting film for reproduction.

2.2.5.1 Head

Rough head drawings were made with the aid of a camera lucida attached to a Wild M5 stereoscopic microscope, at a magnification of 50X. Rough drawings were redrawn before inking so parts could be reoriented and details altered to best represent the species, and to show characteristics of each species in comparable positions.

For male head figures, setae of the ocellar triangle and postcranium were not drawn. To simplify the task of drawing male and female heads of all species, setae were drawn on male head illustrations only.

With large variation in eye height and flagellomere 1 and proboscis lengths within species, head figures should be consulted in conjunction with the Hubbs-Hubbs diagrams to avoid reliance on the figured characteristics of each species.

The rostrum and proboscis are shown in a variety of positions. The rostrum is externally membranous so its shape has no taxonomic value. The prementum of the proboscis is shown as a straight cylindrical structure, for in life it is inflexible. This is not true of the labella, the distal half of which is highly manoeuverable in live specimens. This flexibility is evident in its twisted nature in a few drawings, but generally I drew labella fairly straight to keep drawings standardized. Proboscises as drawn are meant to convey relative differences in length, not shape or structure.

2.2.5.2 Genitalia

Genitalia were temporarily mounted on slides in glycerine jelly[2] for illustrative purposes. Once drawings were completed genitalia were washed free of jelly in hot water and returned to glycerine for storage.

Genitalia should not be left for extended periods in glycerine jelly or their clear extraction becomes difficult; ie. the jelly loses its ability to mix freely with hot water and remains coated to the specimen.

A Leitz SM-LUX compound microscope with drawing tube was used at a magnification of 100X for rough drawings of all genitalic figures. Rough drawings were redrawn and reoriented for better representation of parts, as mentioned for heads.

I was unable to detect setal differences in male and female genitalia useful for distinguishing species, so setae were not illustrated.

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[2] formula of Pantin (1969).

All sclerites of female *Siphona* genitalia from sternum 5 to cerci are shown in Fig. 12. Note that dorsally interrupted tergum of segment 8 is all that remains of terga 6 to 10. Sternum 9 is either lost, or fused with sternum 10.

Figures of male genitalia show only those structures associated with the postgenitalia (segments 9 to 11). In addition to vestiture, the ejaculatory apodeme and paramere (postgonite) are excluded from illustrations.

I do not recommend comparison of figured male genitalia on the basis of structures illustrated but not discussed in the text, for differences may be misleading. For instance, hypandrial and aedeagal apodemes and epandrium are considerably varied intraspecifically, so their figured appearance should not be used for identification purposes. Genitalia were drawn as they were to represent taxonomically useful characters in their proper relative positions as parts of a functional complex.

2.2.5.3 Other structures

Thoracic and abdominal dorsa (Figs. 2, 7-8) were drawn as described for heads. Hairs, which sparsely cover both regions, were not drawn.

Acropods (Figs. 4-6) and the wing (Fig. 3) were drawn with the aid of a drawing tube attached to a SM-LUX compound microscope. Acropods were suspended in glycerine jelly and drawn at a microscope magnification of 400X. Acropod drawings were photo-reduced before inking on mylar drafting film. Short hairs on claws, pulvilli and tarsomere 5 are not shown.

The wing (Fig. 3) was mounted in Canada balsam and drawn at a microscope magnification of 100X. Costal setulae and wing hairs were not illustrated.

2.2.6 Terms

A variety of terms apply to the same structures of adult flies. This developed partly from gradual introduction of new terms by successive generations of dipterists, and partly by establishment of terms unique to particular groups.

With the recent publication of the "Manual of Nearctic Diptera, Volume 1", an attempt was made to standardize terms for structures of adult Diptera (McAlpine, 1981). The depth and detail that pervade this work prompted me to abandon the more familiar terms for tachinids of Crosskey (1973, 1976a) and others in favour of it. Certain of McAlpine's terms are controversial, and for that reason unacceptable to all, yet acceptance of his work in principle would lead to establishment of a unified system of names for structures.

Most structures to which I refer in the text are labelled in Figs. 1-12. Where possible abbreviations correspond to those in the "Manual of Nearctic Diptera". The Manual should be consulted for structures not figured. In a few instances I included a familiar term in parenthesis after a Manual term if the feature was not figured.

One of my two deviations from terms in the Manual involves a few thoracic setae. I retained use of "humeral" and "presutural" setae. The former was termed "postpronotal" in the Manual, but this is unsatisfactory without a replacement name for the posthumeral seta, which was not mentioned in the Manual. I see no reason to incorporate the presutural seta into the supra-alar row, so I disregarded this change.

Certain descriptive terms in the text require explanation to avoid misinterpretation. First of these is colouration, which is difficult to describe qualitatively. This is compounded in *Siphona*, as in most calypterate flies, by the effect pruinosity has on ground colour - where pruinosity [pollinosity] refers to "a nap-like covering to any part of the body formed by closely aggregated ultramicroscopic pubescence" (Crosskey, 1973: 19), and ground colour simply refers to hue of sclerites.

Both pruinosity and ground colour contribute to *Siphona* colouration, but separately described impart little meaning. Therefore I describe "surface colour", which I define as the hue or hues perceived as a result of light reflected from pruinosity as seen against ground colour. This is essentially synonymous with "colour" of most authors, but here permits distinction between ground and surface colour. In the text, where neither surface nor ground colour is specified, surface colour is implied.

Wing colour is varied specifically, but appears very faint from dorsal aspect. To obtain wing colour used in descriptions, I viewed wings from an acute angle to increase colour density and permit differentiation of yellow, brown and cinereous hues.

Less ambiguous than colour but requiring explanation are terms used in describing macrotrichia. Here I diverge from the Manual again. I classify macrotrichia as hairs, setulae and setae (bristles). Hairs are macrotrichia of approximately equal diameter along their lengths. Setulae and setae are macrotrichia with thick bases and slender tips, inserted in conspicuous sockets. Setulae and setae are qualitatively separated on basis of size; setulae being small setae.

I make use of the terms "weak" and "strong" setae in descriptions. This avoids repeated reference to the length and thickness aspects of setal size, both of which are implied by these terms.

Leg setae are named for their positions relative to body axis when leg is fully extended to side. Abbreviations used in description of the genus are as follows:

a - anterior

ad - antero-dorsal

av - antero-ventral

d - dorsal

p - posterior

pd - postero-dorsal

pv - postero-ventral
v - ventral

2.2.7 Notes on descriptive format

2.2.7.1 General

Genus and species descriptions are presented in a uniform format, with the same style and headings. Differences concern degree of coverage. The aim of the genus description was to describe in detail the attributes of *Siphona*, without differentiation between character states shared with other genera and states unique to *Siphona*.

Siphona species descriptions do not repeat non-varied attributes of the genus. In most instances a character or set of characters was described in full for each species unless it is shared with a closely related species. For a few characters in which one state is shared by most species, that state was described as average, and average was described in the genus description.

Certain characteristics are more useful than others for identification purposes, so a diagnosis is presented prior to each description under the heading "Recognition", summarizing those attributes by which the species is most reliably recognized. Also included under this heading is a comparison of the described species with other species with which it may be confused.

2.2.7.2 Specimen label data

Label data for holotypes and allotypes of new species, and examined type material of described species are presented in a uniform manner. Labels are cited in full, following closely the style of Arnaud (1979). Under this system labels are listed from the top down, with data from each label enclosed in quotation marks. Original spelling and punctuation are preserved, and label lines are delimited by a slash mark(/). Deposition of each specimen is given in parenthesis.

Paratype data of new species were treated less stringently than the above. A standardized format was adopted to increase readability and reduce likelihood of errors. Countries and provinces, or states, are arranged alphabetically, counties, cities, etc. are not. Counties (if given on label) are followed by locality, date of collection, collector and number of males and/or females examined. Specimen repositories are given at the end of each paratype list.

Date of collection is given in order of day, month, year, with month in roman numerals and year abbreviated to the last two digits (though written in full if earlier than 1900). Specimens collected in the same locality on different dates by the same collector are cited together, with commas between dates of collection. Inclusive dates of collection are indicated by dashes. For example, 5,7-9.VII.81 means specimens were collected on the 5th of July and again between the 7th and 9th of July, 1981.

I have not presented data about examined, non-type specimens of described species, considering their value insignificant in light of the distribution maps and chart of adult seasonal occurrence. For the sake of posterity a list of these specimens was prepared and deposited in the Archives of the University of Alberta. The list format follows that used for paratypes of new species.

2.2.8 Distribution maps

Localities represented by specimens I personally examined are indicated by dots on the maps. I excluded published locality records because of their unreliability as to species collected.

Only New World records of species described herein are mapped. Holarctic species are indicated as such in figure captions and under heading "Distribution" following descriptions.

2.2.9 Genitalia dissections

Dissections were required to permit examination of *Siphona* male and female genitalia. The technique described below refers to dissection of male genitalia from dried specimens, though it works as well with female and fresh material, with obvious minor changes. This method differs slightly from those reported elsewhere (eg. Beneway, 1963; Wilder, 1979), and was developed to its present form during the course of this study.

Dissection of male genitalia involved removal and slight clearing of the abdomen, extraction and clearing of the genitalia, separation of pre- and postgenitalic structures, and replacement of abdomen on specimen. Details of this procedure follow.

Removal of an abdomen from a dried specimen was relatively easy because it naturally tends to break at its connection to the thorax when gently pushed from below. Gentle prodding from above and from side to side helped detach the abdomen cleanly and evenly.

The abdomen was placed in a solution of about 10% NaOH until the cuticle became flexible (about 10 minutes, but varied from specimen to specimen). I released trapped air from the abdominal cavity during this time (by gentle squeezing) so the membranes around the genitalia would soften from within as well as from without. This had to be done carefully and after some flexibility had been attained, or preabdominal sclerites pulled apart. The abdomen was then transferred to 20% acetic acid to neutralize the base.

Dissection of the genitalia was done in the acetic acid solution. I used the bent and blunted tip of an insect pin, attached to a handle, to hold the abdomen ventral side up against the dish bottom. In this position only a few minutes were required to slice around syntergosternum 7+8 and sternum 5, and pull them and enclosed postgenitalia (segments 9 to 11) free. This operation worked well with a very sharp tungsten steel needle. If tissues were not sufficiently cleared, the preabdominal terga were easily torn; if overcleared there was danger of the terga separating.

The genitalia were returned to the NaOH solution until attached membranous tissue changed from translucent to transparent. This step would take from 5 to 20 minutes, depending on the specimen.

The preabdomen was taken through 10 minute washes of 70% and 95% ethyl alcohol to toluene. After 20 minutes it was removed, air dried (a matter of seconds) and affixed with shellac glue to the thorax of the specimen from whence it came. Slight shrivelling of the preabdomen usually occurred, but I have been unable to devise a procedure that eliminates this. The toluene step (for which similar solvents can be substituted) yielded better results than the traditional method of alcohol steps only.

Sufficiently cleared genitalia were transferred through 5-10 minute washes of 20% acetic acid, 70% and 95% alcohol to glycerine.

The high viscosity of glycerine facilitated separation of the epandrium from syntergosternum 7+8. This accomplished, the postgenitalia were easily removed from the ring-like pregenital segments.

During the course of this study more than 400 male and about 25 female genitalia of *Siphona* and related siphonines were dissected. Since study of male genitalia figured prominently in development of my *Siphona* species concepts, they needed to be readily accessable. To suit this end small vials 1cm in diameter were cut to a height of 7mm and stored in specially constructed trays measuring about 6.5x6.5x1.5cm (outside dimensions). Each tray was fitted with a lid, and held 20 vials in 4 rows. To the pin of each dissected specimen a numbered label was attached, and a corresponding number placed with the genitalia in the vial of glycerine. Genitalia were not placed in microvials and stored with their respective specimens until the study was completed.

Use of these trays reduce time otherwise wasted removing sclerites from microvials, and encourages study of large series of genitalia at a time. If properly used, code numbers do not become mixed. A list of all specimens dissected, with number, label data, sex and species (if known) facilitates reassociation of specimen and genitalia at any time.

3. GENUS SIPHONA MEIGEN

3.1 Aspects of life history

3.1.1 Siphona immatures

Larval instars of *Siphona* species live as internal parasitoids of certain other larval insects. Adult females do not produce many eggs (50-100 in those for which this information is known), which are retained in an elongate, coiled uterus until they have transformed into active larvae (*S.* [?]*cristata*, Roubaud, 1906 and Pantel, 1910; undetermined species, Townsend, 1934; *S. multifaria* and *S. maculata*, personal observation). They are then deposited onto hosts. Larvae bore through host integument and feed within the haemocoel, meanwhile procuring air *via* a posterior connection to a host trachial tube (Roubaud, 1906; Pantel, 1910). When fully mature, *Siphona* larvae abandon their hosts to seek pupation sites in the ground.

3.1.2 Hosts

Hosts of *Siphona* species are inadequately known. *S. geniculata* has been recorded from *Tipula paludosa* Meigen and *T. oleracea* L. in Europe (Rennie and Sutherland, 1920). Also recorded from tipulid larvae are *S. hokkaidensis* (*T. irrorata* Meigen, Mesnil, 1965) and *S. cristata* (*T. maxima* Poda [as *T. gigantea* Schrank], Roubaud, 1906). In addition to the tipulid host, *S. cristata* has been recorded from ca. 15 noctuid species (see Herting, 1960). However, *S. cristata* has been confused with *S. flavifrons* Staeger (and possibly others), so all records are suspect.

Siphona maculata has been reared from larvae of *Agrotis obelisea* and *A. candelisequa* (Herting, 1960). Also recorded from noctuids are the European species *S. collini* and *S. confusa* (Mesnil, 1965), the Mexican species *S. futilis* (as *Bucentes ceres* (Curran, 1932)), and *S. pseudomaculata* Blanchard from South America (Blanchard, 1963).

3.1.3 Adult seasonal occurrence

A chart of adult *Siphona* seasonal occurrence is presented in Fig. 17. Most species span three or more months, though I suspect this is an artifact of supraposition of data from the entire geographic range of a species, rather than an indicator of long adult life or overlapping generations. Indeed, populations near Edmonton with which I am familiar have one generation per year, and adults are seen for only about one month (*S. cristata, maculata* and *multifaria*). *S. geniculata*, the only species for which generation time has been reported, is bivoltine.

Fig. 17 indicates trends; that is, which species are likely to be found in early spring, which are fall species, etc. As such the chart doubles as a check during identifications, although its value in this respect is limited for species with inadequate data.

3.2 Reclassification

Siphona is remarkably well-defined for a genus with more than 80 described species. The long geniculate proboscis is generally a reliable generic characteristic that permits *Siphona* specimens to be identified as such with relative ease. However, possession of a *Siphona*-like proboscis has led to inclusion of a few species in *Siphona* that belong elsewhere. In this section I discuss removal from *Siphona* of eight species that superficially resemble *Siphona* but are more closely related to other taxa[3], and synonymize one genus with *Siphona*.

In 1890 van der Wulp described *Siphona diluta* and *S. futilis*. The syntype series of both species were examined, and *S. futilis* is retained as a valid *Siphona* species. *S. diluta* Wulp is only distantly related to *Siphona*, belonging to *Clausicella* Rondani.

I remove the genus *Siphonopsis* Townsend from *Siphona*, with type-species *S. plusiae* (Coq.), and two other species, *S. brasiliensis* Tnsd. and *S. conata* Rnh. The proboscises of members of *Siphonopsis* are slightly elongate, with labella folded back against, but shorter than, prementum, and shorter than eye height. The labella bear pseudotracheae to their base, unlike the *Siphona* condition wherein the basal half of the labella is fused into a cylindrical sheath.

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[3] excluded from consideration are *Siphona* species not examined during this study; see world list below for species examined.

The male genitalia of *Siphonopsis* species are similar to *Siphona* except the aedeagus is long and thin and the antero-lateral arms of sternum 5 of adults are hooked inward. A very few *Siphona* species have similar fifth sterna (*S. oligomyia* n. sp. (Fig. 11), *S. cuthbertsoni* Curran, and perhaps others I did not examine), but these are almost certainly apotypic and developed independently of *Siphonopsis*.

Recognition of *Siphonopsis* is expedient. The three described species are closely related, but the generic description does not easily accommodate numerous Mexican and Neotropical species that are yet undescribed. The problem lies not with separation of *Siphonopsis* and *Siphona*, but in elucidation of the relationships among *Siphonopsis*, *Pseudosiphona* Tnsd., *Ceranthia* R.D., *Aphantorhapha* Tnsd. and *Asiphona* Mesnil. Especially in the New World this group is inadequately known and in need of revision. Further study may reveal that *Siphonopsis* and perhaps others are best regarded as subgenera of *Ceranthia*.

Two species described from Burma, *Crocuta malaisei* Mesnil and *Crocuta pellex* Mesnil, belong to a group of *Actia* species whose adults possess a long geniculate proboscis (including *A. siphonosoma* Malloch, *A. jocularis* Mesnil, *A. triseta* Mesnil and perhaps others with which I am unfamiliar). In a few species the structure of the proboscis of adults is amazingly like that in *Siphona*, representing an excellent example of parallel evolution. In other respects these *Actia* species are characteristic of that genus.

Mesnil recognized his error and briefly mentioned *C. malaisei* and *C. pellex* as *Actia* species in his description of *A. jocularis* (1957: 47), and again in his treatment of Palearctic *Actia* (1963: 813).

Crosskey examined the types of both *C. malaisei* and *C. pellex* and placed both species back into *Siphona* (1976a: 214). I have examined a male and female specimen of *C. malaisei* and I agree with Mesnil's placement of this species in *Actia*. From the description of *C. pellex* and Mesnil's remarks concerning it, I am confident it, too, belongs in *Actia*.

Two other species described from Burma, *Crocuta alticola* Mesnil and *Crocuta crassulata* Mesnil, are placed in *Ceranthia s. lat*. Adults of both species have prementum and labella elongate, as in *Siphona* species, but the labella bear pseudotracheae along their lengths, as in *Siphonopsis* adults. The male genitalia are distinctly *Ceranthia*-like, with broad surstyli (slender in *Siphona* species) and a single short posteriorly directed seta on each gonite (long in other examined *Ceranthia* spp., absent from all examined *Siphona* spp).

I refer to *Ceranthia* in the wide sense because the genus has traditionally been comprised only of adults with an average-sized proboscis and very reduced (apotypic) palpus. The palpi of *C. alticola* and *C. crassulata* adults are average-sized, but I consider the male terminalia with its complex structures more suitable for generic decisions. I include *Asiphona* in *Ceranthia s. lat.*, for I am unaware of any synapotypies that unite *Asiphona* species. *Asiphona* is apparently comprised of species that are close to, but do not belong in, *Ceranthia s. str.*

To *Siphona* I add one genus, *Phantasiosiphona* Tnsd., with type-species *P. tropica* Tnsd. and one other species, *P. kuscheli* Cortés. Given the spectrum of specific attributes within *Siphona*, *P. tropica* is not extraordinary, and does not rank even subgeneric status. *P. kuscheli* also conforms to the generic description of *Siphona*.

In summary, species removed from *Siphona*, with their new combinations, are as follows:

Siphona alticola (Mesnil), 1953: 110 (*Crocuta* (*Siphona*)), Burma = *Ceranthia alticola*.

Siphona brasiliensis (Townsend), 1929: 374 (*Siphonopsis*), Brazil = *Siphonopsis brasiliensis*.

Siphona conata (Reinhard), 1959: 162 (*Siphonopsis*), Calif. = *Siphonopsis conata*.

Siphona crassulata (Mesnil), 1953: 112 (*Crocuta* (*Siphona*)), Burma = *Ceranthia crassulata*.

Siphona diluta van der Wulp, 1890: 126 (*Siphona*), Mexico = *Clausicella diluta*.

Siphona malaisei (Mesnil), 1953: 110 (*Crocuta* (*Siphona*)), Burma = *Actia malaisei*.

Siphona pellex (Mesnil), 1953: 111 (*Crocuta* (*Siphona*)), Burma = *Actia pellex*.

Siphona plusiae Coquillett, 1895: 125 (*Siphona*), Calif. = *Siphonopsis plusiae*.

3.3 Generic synonymy of Siphona Meigen

A complete list of references to each of the following names was not attempted. Rather, only major catalogues and literature with keys or descriptions pertaining to New World *Siphona* species are cited. Published state records are largely inaccurate and are not included.

Crocuta Meigen, 1800: 39. Type-species, *Musca geniculata* De Geer (Coquillett, 1910: 528). Suppressed by I.C.Z.N., 1963: 339 (Opinion 678).-- Townsend, 1919: 584.

Siphona Meigen, 1803: 281. Type-species, *Musca geniculata* De Geer, 1776, by designation of I.C.Z.N., 1974: 157 (Opinion 1008) (see Sabrosky, 1971, for discussion of the history of *Siphona* nomenclature).-- Wulp, 1890: 125.-- Townsend, 1891: 368.-- Coquillett, 1897: 75.-- Aldrich, 1905: 444.-- Curran, 1933: 10.-- Curran, 1934: 455.-- Aldrich, 1934: 108.-- Townsend, 1936: 150.-- Townsend, 1940: 292.-- Reinhard, 1943: 20.-- Sabrosky and Arnaud, 1965: 1063.-- Cole, 1969: 519, 570.-- Cortés and Hichins, 1969: 57.-- Cortés and Campos, 1970: 98.-- Guimarães, 1971: 170.-- Arnaud, 1978: 458.

Bucentes Latreille, 1809: 339. Type-species, *B. cinereus* Latreille (monotypy) = *S. geniculata* (De Geer).-- Curran, 1932: 13.

Phantasiosiphona Townsend, 1915: 93. Type-species *P. tropica* Townsend (original description).-- Townsend, 1936: 150, 1940: 286.-- Cortés, 1952: 110.-- Guimarães, 1971: 169. **New synonymy.**

3.4 Generic description of *Siphona* Meigen

The following generic diagnosis and description are based on study of adult specimens of North American *Siphona* species. A few species from other regions do not fit this generic description in all characteristics.

Recognition.-- Small flies with narrow clypeus, subquadrangular head in profile and a long, geniculate proboscis. Labella slightly longer than prementum, in most species longer than eye height. Second aristomere elongate, at least 2.5X longer than wide. Anal vein extended to wing margin at least as fold. R_{4+5} setulose dorsally between bifurcation of R_{2+3} and R_{4+5} and crossvein r-m (beyond crossvein in *S. lutea*). Three katepisternal (sternopleural) setae, antero-ventral as strong as or stronger than antero-dorsal. Most species with light coloured pruinosity, particularly on preabdomen, a few species darker but not black. Femur and tibia predominantly yellow in most species, tarsi brown to black. Preabdomen without discal setae, T_{1+2} with or without one pair each strong median and strong lateral marginal setae. Female genitalia unmodified (Fig. 12). Male genitalia as in Figs. 1,60-80.

Description.-- *Length:* 3.0-6.5mm.

Male. *Head* (Figs. 1,18-40). *Front:* wider than high, 1.1-1.3 head height; clypeus narrowed, parallel-sided; distance between vibrissae less than half head width (0.33-0.45).

Profile: subquadrangular; higher than wide, width at antennal axis 0.60-0.75 head height; frons slightly convex, lower anteriorly; face vertical to slightly retreated, lower margin protruded beyond vibrissal angle; angle at scape between frons and facial ridge in most species sharply defined, in a few species broadly rounded; width of parafacial and gena wide or narrow, inversely proportional to eye size.

Colouration: frontal vitta orange or yellow to testaceous, brown or reddish-brown; face, parafacial, gena and lower third or less of postcranium light in ground colour, surface white or light yellow to light brown; ground colour of fronto-orbital plate and upper postcranium light to dark, surface colour varied markedly, from yellow or gold to brown or dark brown, darkest on orbital plate; ocellar triangle dark in ground colour, surface brown to dark brown; antenna very varied, yellow to black; palpus entirely yellow in most species, apex infuscate in a few species; proboscis very varied, yellow to black.

Eye: bare or nearly so; size very varied, small to large, slender to broad, widest at or above center, narrowed below center or evenly rounded along anterior margin; eye height 0.627-0.911 head height (Fig. 13), average height for genus between ca. 0.73-0.82 head height.

Macrotrichia: five frontal setae, medio-reclinate, lowermost seta laterad insertion of flagellomere 1; 2nd and 4th frontal setae stronger than 1st, 3rd and 5th; 2 reclinate orbital setae in line with and above frontal setae, lower seta intermediate in strength between largest frontal seta and inner vertical seta, upper seta latero-reclinate, in strength intermediate between shortest and longest frontal setae; 2 proclinate orbital setae, subequal in size, not larger than largest frontal seta, laterad frontal and reclinate orbital setae; lower reclinate orbital seta halfway between proclinate orbital setae to laterad upper proclinate orbital seta, position intraspecifically varied; inner vertical seta well-developed, subequal in size to vibrissa; outer vertical seta latero-reclinate, subequal in size to lower reclinate orbital seta [appears shorter in most figures because of its inclination]; ocellar triangle with 1 pair latero-proclinate ocellar setae and several hairs; postocellar setae divergent or parallel; paravertical seta subequal in size to setulae of postocular row; postcranium uniformly and sparsely haired; upper parafacial and fronto-orbital plate sparsely haired with less than 10 hairs in most species, to 15 or 20 in *S. lurida* and *S. geniculata*; vibrissal angle with 2-10 setae in addition to vibrissa, and 1 to several hairs, average for genus 1 seta laterad or above vibrissa and 1 below, and 2 or 3 hairs; 1 subvibrissal seta on antero-ventral margin of gena; aristomere 3 micropubescent; palpus with 2 or 3 setulae on lower surface, and several hairs; proboscis sparsely haired.

Antenna: flagellomere 1 extremely varied in length among species, 0.403-0.740 head height (Fig. 14); shape of flagellomere 1 in profile from short and slender or broad, to long and slender or broad; length of aristomere 2 proportional to size of flagellomere 1, in most species between 2.5-6.0 times longer than wide, up to 8 times longer than wide in species with very long first flagellomeres (eg. *S. tropica*, *S. pisinnia* and *S. lurida*); length of aristomere 3 0.50-0.65 head height in most species, shorter (0.35-0.45) in most specimens of *S. hokkaidensis*, *S. geniculata* and *S. medialis*; in all species except *S. hokkaidensis*, aristomere 3 not thickened beyond basal half, distally tapered to a fine tip, in *S. hokkaidensis* aristomere 3 thickened almost to tip in most specimens.

Mouthparts: maxillary palpus slightly clavate, length 0.35-0.55 head height; labella elongate, straight at least on basal half, apical 0.25 (on species with a long proboscis) to 0.5 (species with a short proboscis) flexible in live specimens, twisted on most dried specimens; proboscis length [combined lengths of prementum and labella] varied from 1.3-3.2 head height (Fig. 15), average for genus between ca. 1.8-2.5 head height.

Thorax (Fig. 2). *Colouration:* average colouration for genus: ground colour black, with humeral callus and apex of scutellum light in ground colour in most specimens; dorsum blue-gray or gray anteriorly, mixed with brown on posterior prescutum, scutum and scutellum; amount of brown varied within and among species, in most species 3 faint to distinct brown vittae visible on posterior prescutum and scutum; ground colour more apparent on pleura than dorsum, such that light reflected from light gray, blue-gray, yellow or light brown pruinosity and black ground colour produces a sheen - pleura alternately appearing light or dark as specimen rotated. A few species differ from average colouration in possessing yellow thorax (in ground and surface colour). Wing tegula yellow to black; wing membrane yellowish, cinereous or brownish hyaline. Legs, average for genus: femora yellow, or predominantly yellow and distally reddish-brown on mid- and hindlegs and varied amounts of reddish-brown on dorsal and posterior surfaces of foreleg (intraspecifically varied); tibia yellow, or predominantly yellow and basally reddish-brown when femur reddish-brown distally. A few species with greater than average amounts of reddish-brown on femora and tibia, or fuscous overall. Tarsi brown to black.

Macrotrichia: setae on prescutum and scutum: acrostichal (weak) 2-3 [presutural], 3-4 [postsutural]; dorsocentral 2-3, 3-4; intra-alar 1,3; supra-alar 3; humeral 2; posthumeral 1; presutural 1; notopleural 2; postalar 2. Scutellum: strong basal, lateral and subapical, weak apical and discal. Pleura: proepisternal (propleural) 1; proepimeral (prostigmatic) 1; anepisternal (mesopleural) row; anepimeral (pteropleural) 1 (weak); katepisternal (sternopleural) 3, postero-dorsal very strong, others weaker, antero-ventral slightly longer than antero-dorsal; meral (hypopleural) row of 3-4; katepimeron (barette) and anatergite (mediotergite) bare. Sterna: prosternum with a single pair of setulae in most specimens, bare in a few (or single setula on one side only). Foreleg: femur, *pd* row of 3-5 setae; *pv* surface with 1 to several setae, strongest seta subadjacent to distal *pd* seta. Tibia, *ad* and *pd* surfaces each with row of 2-5 setae; *p* seta ca. 0.4 tibial length from apex; preapical setae, well-developed *d* and *pv*, *pd* and *v* weak or absent. Midleg: femur, 2 adjacent *a* setae at midpoint; ca. 0.1 femoral length from apex, well-developed *pd* and *p* setae, weak *ad* seta; sparse row of setulae on *pv* surface, with 1 strong setula or seta 0.25 femoral length from base. Tibia, *ad* seta slightly distad of midpoint; 2 *pd* setae, ca. 0.3 and 0.6 tibial length from base; *v* seta ca. 0.6 tibial length from base; preapical setae, well-developed *ad*, *v* and *pv*, other setae, if present, weak. Hindleg: femur, *ad* row of setae, increasing in strength apically; very strong *av* seta ca. 0.25 femoral length from apex; 2 *v* setae basad of midpoint; *pd* seta ca. 0.1 femoral length from apex. Tibia, *ad* and *pd* surfaces each with row of 4-6 setae, alternating weak and strong; 3-5 *av* setae from ca. 0.4-0.7 tibial length from base; preapical setae, *d*, *ad*, *pd* and *av*.

Acropod (Figs. 4-6): claws and pulvilli varied in size, subequal on all legs; length of each claw and pulvillus from ca. width of tarsomere 5 (ie. averaged-sized, Figs. 4,6) to ca. length of tarsomere 5 (ie. large, Fig. 5).

Wing (Fig. 3): short and broad; Sc incised adjacent to subcostal break; apices of R_{4+5} and M closely approximated or contiguous in wing margin, slightly anterior to wing tip; anal vein (A_1) reaching wing margin at least as fold; R_1 bare dorsally except for a few species which have 1 or 2 setulae on bend of R_1; R_{4+5} dorsally with row of 3-10 setulae between bifurcation of R_{2+3} and R_{4+5} and crossvein r-m; setulae extended beyond crossvein r-m in most specimens of *S. lutea*; CuA_1 bare dorsally except for 1-3 setulae in a very few specimens of *S. lutea*; single setula ventrally at bifurcation of R_{2+3} and R_{4+5}.

Preabdomen (Figs. 7-8). Ovoid to slightly elongate in dorsal view; middorsal depression extended to middle of

T_{1+2}.

Colouration: very varied intra- and interspecifically; most species dorso-medially vittate, average pattern T_4 and T_5 black in ground colour, vitta on T_{1+2} and T_3 (width averaging distance between median marginals on T_3), rest of preabdomen yellow in ground colour; areas black in ground colour with surface blue-gray, gray, brownish-gray or brown, dark brown to black around macrotrichial insertions; areas yellow in ground colour with surface yellow, light brown or tawny. Preabdomen entirely black in ground colour in a few species, at least dorsally and laterally, or with very reduced areas of yellow ground colour on extreme lateral edge of T_{1+2} and antero-lateral edge of T_3; Preabdomen entirely yellow in ground and surface colour in a few other species.

Macrotrichia: discals absent; T_{1+2} without median marginals in most species, 1 seta on one side or 1 pair present in a few species; T_{1+2} with 1 pair strong lateral marginals in most species (ca. 0.75 length of lateral marginals on T_3 or longer), weak pair in a few species (less than 0.5 length of lateral marginals on T_3), 2 pair strong lateral marginals in a few specimens of a few species; T_3 with 1 pair each strong median and lateral marginals in most species, a few specimens of a few species with 2 pair lateral marginals; T_4 with 3 pair marginals; T_5 with 3-5 pair marginals.

Genitalia (Figs. 9,60-80). Epandrium in profile saddle-shaped, slightly higher than long, antero-lateral margin with medially-angled flange; hypandrial apodeme articulated with antero-ventral margin of epandrium; gonite sub-triangular, with a flange produced ventro-laterally; paramere lobe-like, ca. twice as long as wide; surstylus narrow, apex even with or extended beyond apex of cerci; cerci fused medially along lower half, long and narrow, smoothly tapered with slight inflexion at midpoint, apex curved anteriorly; epiphallus not developed.

Aedeagus: distiphallus in profile triangular to quadrangular, surface finely dentate, antero-ventral margin from dentate to bearing well-developed hooks; angle of distiphallus from even with angle of basiphallus (eg. *S. illinoiensis*) to sharply bent downward (eg. *S. intrudens*); apex in profile from narrow (eg. *S. tropica*) to broad (eg. *S. medialis*).

Sternum 5 (Figs. 10-11): posterior margin U-shaped (not V-shaped as in most *Actia* species); notched postero-medially; all species except *S. oligomyia* with postero-lateral arms smoothly curved around posterior margin, *S. oligomyia* with arms hooked inward.

Female. As described for male except as follows.

Head (Figs. 41-59). Eye and flagellomere 1 smaller than in male; female palpus of a few species longer than in male.

Thorax. *Acropod:* smaller than in males; most species with large claws and pulvilli in male have only slightly larger than average claws and pulvilli in female.

Preabdomen. *Colouration:* same range as described for male; female darker than male in most species; females of species with vittate males in most species with more extensive areas of black ground colour than males, vitta shorter and broader than in males, or absent.

Genitalia (Fig. 12). Unmodified; structurally very similar among *Siphona* females; terga 6, 7, 9 and 10 lost; tergum 8 dorsally interrupted; sternum 9 lost, or fused with sternum 10; cerci well developed (ref. Herting, 1957); two spermathecae.

3.5 World list of Siphona species

This list is inclusive of all *Siphona* species described before August, 1981, plus those described as new herein. The genus in which each species was described is given only if not *Siphona*. A capital letter to left of species name denotes the region from which the species was described with, for a few species, a second letter denoting presence of the species in another region.

Species of which specimens were examined during the course of this revision are so indicated in the list. Unless otherwise stated, specimens examined were not type material. Status of species not examined follows recent revisionary or catalogue placements. New species, synonymies, combinations and lectotype designations are noted.

Types of nominal species of *Siphona* described by Robineau-Desvoidy (1830, 1850) are lost (Herting, per. comm.), and although most were probably conspecific with *S. geniculata*, their status cannot be verified so the names are treated as *nomina dubia*.

Regional code:

A Afrotropical, *sensu* Crosskey and White, 1977.

N North America.

O Oriental, *sensu* Crosskey, 1976a.

P Palearctic, as limited by Afrotropical and Oriental regions in their present interpretation.

S South America.

I examined specimens of a new species of *Siphona* from Australia, but as yet no *Siphona* have been described from the region. The tribe Siphonini is apparently not represented in New Zealand (Dugdale, 1969).

A *abbreviata* (Villeneuve), 1915: 199 (*Bucentes*) [examined].

N *akidnomyia* new species.

A *albocincta* (Villeneuve), 1942: 55 (*Bucentes*) [examined].

A *amoena* (Mesnil), 1952: 12 (*Crocuta*) [examined].

A *amplicornis* Mesnil, 1959: 21.

syn. *nigrohalterata* Mesnil, 1959: 22 (as ssp).

A *angusta* Mesnil, 1959: 22.

A *antennalis* (Mesnil), 1952: 9 (*Crocuta*) [examined].

A *atricapilla* Mesnil, 1959: 20.

A *bevisi* Curran, 1941: 7 [holotype examined].

A *bilineata* (Mesnil), 1952: 10 (*Crocuta*) [examined].

P *boreata* Mesnil, 1960: 190 [holotype examined].

N *brunnea* **new species.**

A *capensis* Curran, 1941: 7.

P *collini* Mesnil, 1960: 188 [holotype examined].

P *confusa* Mesnil, 1961: 201 [holotype examined].

A *cothurnata* (Mesnil), 1952: 17 (*Crocuta*) [examined].

A *creberrima* (Speiser), 1910: 142 (*Crocuta*).

P,N *cristata* (Fabricius), 1805: 281 (*Stomoxys*) [examined].

syn. *chaetolyga* Rondani, 1865: 194.

palpina Zetterstedt, 1859: 6064.

A *cuthbertsoni* Curran, 1941: 7 [holotype examined].

P *efflatouni* Mesnil, 1960: 188 [holotype examined].

P *flavifrons* Staeger *in* Zetterstedt, 1849: 3211 [examined].

N *floridensis* **new species.**

O *foliacea* (Mesnil), 1953: 113 (*Crocuta* (*Siphona*)) [examined].

A *fuliginea* Mesnil, 1977: 77.

ssp. *cerina* Mesnil, 1977: 76.

ssp. *rubea* Mesnil, 1977: 77.

N *futilis* van der Wulp, 1890: 125 [lectotype designated].

syn. *ceres* (Curran), 1932: 14 (*Bucentes*) [holotype examined, new synonymy].

O *gedeana* van der Wulp, 1896: 109.

syn. *nigripalpis* (de Meijere), 1924: 223 (*Bucentes*).

P,N *geniculata* (De Geer), 1776: 20 (*Musca*) [examined].

syn. *analis* Meigen, 1824: 157.

cinerea Meigen, 1824: 156.

cinereus (Latreille), 1809: 339 (*Bucentes*).

meigenii St. Fargeau and Serville, 1828: 501.

minuta (Fabricius), 1805: 282 (*Stomoxys*).

nigrovittata Meigen, 1824: 157.

tachinaria Meigen, 1826: 156.

urbanis (Harris), 1780: 153 (*Musca*).

A *gracilis* (Mesnil), 1952: 13 (*Crocuta*) [examined].

P *grandistylum* Pandellé, 1894: 108 [examined].

P,N *hokkaidensis* Mesnil, 1957: 36 [holotype examined].

syn. *silvarum* Herting, 1967: 9 [holotype examined, new synonymy].

N *illinoiensis* Townsend, 1891: 368 [lectotype designated].

N *intrudens* (Curran), 1932: 14 (*Bucentes*) [holotype examined].

A *janssensi* (Mesnil), 1952: 4 (*Crocuta*) [examined].

S *kuscheli* (Cortés), 1952: 110 (*Phantasiosiphona*)

[examined, new combination].

A *laticornis* Curran, 1941: 9.

A *lindneri* Mesnil, 1959: 22.

N *longissima* **new species.**

N,P *lurida* Reinhard, 1943: 20 [holotype examined].

N *lutea* (Townsend), 1919: 584 (*Crocuta*) **[lectotype designated].**

syn. *tenuis* Curran, 1933: 10 [holotype examined, **new synonymy].**

N *macronyx* **new species.**

P,N *maculata* Staeger *in* Zetterstedt, 1849: 3212 [examined].

ssp. *griseola* Mesnil, 1970: 118 [holotype examined].

P *maculipennis* Meigen, 1830: 365 (unrecognized).

N *medialis* **new species.**

A *melania* (Bezzi), 1908: 58 (*Bucentes*).

A *melanura* Mesnil, 1959: 23.

N *multifaria* **new species.**

A *munroi* Curran, 1941: 6.

A *murina* (Mesnil), 1952: 15 (*Crocuta*) [examined].

P *nigricans* (Villeneuve), 1930: 100 (*Bucentes*) [holotype examined].

A *nigroseta* Curran, 1941: 8.

O *nobilis* (Mesnil), 1953: 112 (*Crocuta* (*Siphona*)).

A *obesa* (Mesnil), 1952: 8 (*Crocuta*) [examined].

A *obscuripennis* Curran, 1941: 8 [holotype examined].

N *oligomyia* **new species.**

N *pacifica* **new species.**

P *paludosa* Mesnil, 1960: 188 [examined].

A *patellipalpis* (Mesnil), 1952: 10 (*Crocuta*) [examined].

P *pauciseta* Rondani, 1865: 193 [examined].

syn. *delicatula* Mesnil, 1960: 190.

oculata Pandellé, 1894: 108.

A *phantasma* (Mesnil), 1952: 7 (*Crocuta*) [examined].

A *pigra* Mesnil, 1977: 78.

N *pisinnia* **new species.**

S *pseudomaculata* Blanchard, 1963: 233.

A *reducta* (Mesnil), 1952: 18 (*Crocuta*) [examined].

ssp. *ludicra* Mesnil, 1977: 78.

N *rizaba* **new species.**

P *rossica* Mesnil, 1961: 202 [examined].

A *rubrapex* Mesnil, 1977: 79.

A *rubrica* (Mesnil), 1952: 11 (*Crocuta*) [examined].

A *setinerva* (Mesnil), 1952: 16 (*Crocuta*) [examined].

P *setosa* Mesnil, 1960: 191 [examined].

P *seyrigi* Mesnil, 1960: 189 [holotype examined].

A *simulans* (Mesnil), 1952: 18 (*Crocuta*).

S *singularis* (Wiedemann), 1830: 335 (*Tachina*) (unrecognized).

A *sola* Mesnil, 1959: 21 [examined].

A *spinulosa* (Mesnil), 1952: 12 (*Crocuta*) [examined].

A *trichaeta* (Mesnil), 1952: 18 (*Crocuta*) [examined].

N,S *tropica* (Townsend), 1915: 93 (*Phantasiosiphona*) [paratype examined, new combination].

A *unispina* (Mesnil), 1952: 14 (*Crocuta*) [examined].

syn. *infuscata* (Mesnil), 1952: 14 (*Crocuta*, as ssp.).

A *vittata* Curran, 1941: 8 [holotype examined].

A *vixen* Curran, 1941: 9 [holotype examined].

A *wittei* (Mesnil), 1952: 5 (*Crocuta*) [examined].

NOMINA DUBIA

analis Robineau-Desvoidy, 1830: 92.

clausa Robineau-Desvoidy, 1850: 209.

consimilis Robineau-Desvoidy, 1850: 205.

fuscicornis Robineau-Desvoidy, 1850: 205.

humeralis Robineau-Desvoidy, 1850: 207.

melanocera Robineau-Desvoidy, 1850: 206.

pusilla Robineau-Desvoidy, 1830: 92.

syn. *persilla* Coquillett, 1897: 76 (mispelled reference to *pusilla* Robineau-Desvoidy).

quadrinotata Robineau-Desvoidy, 1850: 203.

syn. *quadricincta* Rondani, 1859: 10 (mispelled reference to *quadrinotata* Robineau-Desvoidy).

silvatica Robineau-Desvoidy, 1850: 208.

testacea Robineau-Desvoidy, 1850, 208.

tristis Robineau-Desvoidy, 1850: 203.

NOMINA NUDA

anthomyformis Lynch Arribálzaga *in* Brauer, 1898: 505

(1898: 13).

dorsalis Brauer and Bergenstamm, 1891: 410.

pauciseta Mesnil, 1964: 856 (as ssp. of *geniculata*).

taiwanica Baranov *in* Hennig, 1941: 195.

3.6 Keys to adults of North American Siphona species

Siphona species are not sufficiently different and are too intraspecifically varied to permit construction of a key based solely on external, diagnostic characteristics. Therefore I found it necessary to frequently employ mensural characteristics (based on data presented in Hubbs-Hubbs diagrams Figs. 13-16) and features of male genitalia in the following keys to North American *Siphona* species. As a consequence, female specimens do not key as accurately as males, and should only be used if male associates are unavailable. Even males of *S. cristata* and *S. multifaria* cannot always be separated (couplet 19'), while a few specimens of other species may be outside the recorded range of variation.

Given certain conditions it should be possible to identify most *Siphona* specimens. Firstly, males are more reliably keyed than females. Secondly, it is advisable to check characteristics of several male specimens of the same species against values given in the Hubbs-Hubbs diagrams to confirm a species identification. Thirdly, "Recognition" section under each species treatment has been included to assist identifications by summarizing key features of a description and contrasting similar species. To simplify keying of North American *Siphona* specimens, species were divided into two geographical groups and keyed separately: (1) species of Canada and the United States, and (2) species of Middle America. *S. pisinnia* is shared between regions and is keyed twice. *S. multifaria* is recorded almost to the Mexican border in the United States, so it is included in the key to Middle American species.

The *Siphona* fauna of Middle America is inadequately known. As more specimens of known species become available the key will probably require modification to incorporate greater intraspecific variation. Similarly, the key will have to be modified for inclusion of currently undiscovered species.

Most terms are as used in the "Manual of Nearctic Diptera, Volume 1" (McAlpine, 1981). See "Terms" section and genus description for information regarding *Siphona* characters.

Figure numbers of male and female head profiles are cited following each species name. Male genitalia of all species are shown in Figs. 9,60-80. The geographical distribution of each species is given as an aid to identification of specimens.

3.6.1 Key to adults of Siphona species of Canada and United States

1. T_{1+2} with one pair strong median marginal setae (Fig. 8) 2

1'. T_{1+2} without median marginal setae (Fig. 7), or one strong seta on one side only, or one pair scarsely differentiated from adjacent marginal hairs. . . .6

2(1). Surstylus with apex even with or extended slightly beyond apex of cerci (Fig. 72); distiphallus slightly or sharply bent downward from angle of basiphallus; specimens from Washington, Idaho, Oregon and California with femora and tibiae reddish-brown to fuscous, specimens from other areas with dorsal and posterior surfaces of fore femur reddish-brown to fuscous in a few specimens, other specimens with legs average (ie. femoral-tibial articulation reddish-brown, rest of femur and tibia yellow); transcontinental, most widely recorded from western USA (Fig. 94) . . . . *S. medialis* n.sp.(Figs. 29,52)

2'. Surstylus with apex extended beyond apex of cerci by more than preapical width of surstylus (Figs. 70-71); slope of distiphallus even with that of basiphallus; leg colouration average 3

3(2'). Male 4

3'. Female 5

4(3). Distiphallus parallel-sided in profile, slender in anterior view (Fig. 70); aristomere 3 tapered to fine tip; flagellomere 1 short and narrow, length of flagellomere 1: head height 0.42-0.48; introduced to, and only recorded from lower, Fraser Valley of British Columbia (Fig. 91). . . . . *S. geniculata* (De G.)(Fig. 28)

4'. Distiphallus slightly broader at base than apex in profile, average *Siphona* width in anterior view (Fig. 71); aristomere 3 thickened to near tip in most specimens; flagellomere 1 varied, from short and narrow to long and broad, length of flagellomere 1: head height 0.43-0.67; transcontinental (Fig. 81)] . . . . *S. hokkaidensis* Mesn.(in part)(Figs. 30-32)

5(3'). Flagellomere 1 with apex truncate in most specimens; transcontinental (Fig. 81) . . . . *S. hokkaidensis* Mesn.(in part)(Fig. 51)

5'. Flagellomere 1 with apex rounded along ventral margin; introduced to, and only recorded from, lower Fraser Valley of British Columbia (Fig. 91) . . . . *S. geniculata* (De G.)(Fig. 50)

6(1'). Body pale yellow overall in ground colour 7

6'. Body reddish-brown to black in ground colour at least on thoracic dorsum. 8

7(6). Male sternum 5 with antero-lateral arms not hooked inward (Fig. 10); proboscis shorter than 2.2X head height; most specimens with R_{4+5} setulose beyond crossvein r-m on at least one side; transcontinental (Fig. 89). . . . . *S. lutea* (Tnsd.)(Figs. 26,48)

7'. Male sternum 5 with antero-lateral arms hooked inward (Fig. 11); proboscis longer than 2.3X head height; R_{4+5} not setulose beyond crossvein r-m; western North America (Fig. 90); female unknown . . . . *S. oligomyia* n.sp.(Fig. 27)

8(6'). Proboscis shorter than 1.8X head height 9

8'. Proboscis longer than 1.8X head height. 13

[*S. intrudens* keyed through both halves of couplet]

9(8). Vibrissal angle with 5-10 setae in addition to vibrissa and several hairs; eye very small, in male less than 0.68 head height; T_{1+2} with strong lateral marginal setae; western USA (Fig. 86) . . . . *S. lurida* Rnh.(Figs. 21,41)

9'. Vibrissal angle with 2-3 setae in addition to vibrissa and several hairs; male eye larger than 0.70 head height; T_{1+2} with weak or strong lateral marginal setae. 10

10(9'). Four postsutural (scutal) dorsocentral setae; distiphallus dentate along antero-ventral margin

(Fig. 61); Florida and southern Georgia (Fig. 84) . . . . *S. floridensis* n.sp.(Figs. 19,43)

10'. Three postsutural dorsocentral setae; distiphallus with several distinct, small or large hooks along antero-ventral margin (Figs. 60,62) 11

11(10'). Male. 12

11'. Female. . . . . *S. maculata* Staeg.(Fig. 42) . . . . and *S. intrudens* (Cn.)(Fig. 44) [separation difficult without male associates; see discussion under *S. maculata*, "Remarks"]

12(11). Distiphallus U-shaped in anterior view, with 3-4 large hooks along antero-ventral margin (Fig. 62); preabdomen black in ground colour overall, or vittate and yellow in ground colour laterally on T_{1+2} and T_3; transcontinental (Fig. 85) . . . .*S. intrudens* (Cn.)(in part)(Fig. 20)

12'. Distiphallus V-shaped in anterior view, with several small hooks (Fig. 60); preabdomen vittate, yellow in ground colour laterally on T_{1+2} and T_3; transcontinental (Fig. 82). . . . . *S. maculata* Staeg.(Fig. 18)

13(8'). Distiphallus U-shaped in anterior view, with 3-4 large hooks along antero-ventral margin (Fig. 62); 3 postsutural dorsocentral setae; T_{1+2} with weak lateral marginal setae in most specimens; proboscis shorter than 2.0X head height; transcontinental (Fig. 85) . . . . *S. intrudens* (Cn.)(in part)(Figs. 20,44)

13'. Distiphallus V-shaped in anterior view, anteroventral margin dentate or with small hooks; 3 or 4 postsutural dorsocentral setae; T_{1+2} with weak or strong lateral marginal setae, if weak (some specimens of *S. pacifica*), then 4 postsutural dorsocentral setae; proboscis longer than 1.85X head height 14

14(13'). Male. 15

14'. Female. 20

15(14). Surstylus with apex extended beyond apex of cerci by more than preapical width of surstylus (Fig. 71); short, thick aristomere 3 (0.35-0.45 head height) in most specimens; most specimens from eastern North America with broad, truncate flagellomere 1 (Fig. 31), specimens from elsewhere with flagellomere 1 varied (Figs. 30,32); transcontinental (Fig. 81). . . . . *S. hokkaidensis* Mesn.(in part)(Figs. 30-32)

15'. Surstylus with apex even with or extended slightly beyond apex of cerci; aristomere 3 of average length (0.50-0.65 head height), tapered to fine tip; flagellomere 1 with shape varied 16

16(15'). Length of flagellomere 1: head height less than 0.50; western USA 17

16'. Length of flagellomere 1: head height greater than 0.50; widely distributed. 18

17(16). Three postsutural dorsocentral setae; tarsal claws large (as in Fig. 5); vibrissal angle with 3-6 setae and several setulae in addition to vibrissa and hairs; distiphallus sharply bent downward from basiphallus, with small hooks on antero-ventral margin (Fig. 75); head with characteristic habitus in profile; recorded from Washington and western Idaho (Fig. 88) . . . . .*S. macronyx* n.sp.(Fig. 33)

17'. Four postsutural dorsocentral setae; tarsal claws of average size (as in Figs. 4,6); vibrissal angle with 2-3 setae in addition to vibrissa and hairs; distiphallus bent slightly downward from angle of basiphallus, dentate on antero-ventral margin (Fig. 64); recorded from California and Washington (Fig. 87) . . . .*S. pacifica* n.sp.(Fig. 22)

18(17'). Proboscis shorter than 2.3X head height; length of flagellomere 1: eye height greater than 0.76; flagellomere 1 fuscous to black; southwestern USA and Mexico (Fig. 83). . .*S. pisinnia* n.sp.(Fig. 23)

18'. Proboscis longer than 2.25X head height, or from central or eastern North America (*S. illinoiensis*); length of flagellomere 1: eye height less than

0.85; flagellomere 1 varied in colour, testaceous to black. 19

19(18'). Distiphallus narrow in profile, apex sloped sharply postero-ventrally in most specimens (Fig. 9); slope of distiphallus even with that of basiphallus in most specimens, slightly bent in a few; proboscis shorter than 2.5X head height; length of flagellomere 1: eye height less than 0.69; central and eastern North America (Fig. 92) . . . .
. . . . *S. illinoiensis* (Tnsd.)(Fig. 1)

19'. Distiphallus broad in profile, apex not sloped sharply postero-ventrally in most specimens (Figs. 66-67); distiphallus bent sharply downward from angle of basiphallus; proboscis longer than 2.25X head height; length of flagellomere 1: eye height greater than 0.65; transcontinental (Figs. 93,95) .
. . . .*S. cristata* (Fabr.)(Fig. 24)
. . . . .and *S. multifaria* n.sp.(Fig. 25)
[see "Remarks" under *S. cristata* for discussion concerning separation of these species]

20(14'). Flagellomere 1 truncate apically; aristomere 3 short (0.35-0.45 head height) in most specimens; transcontinental (Fig. 81). . . . .
. . . . . . *S. hokkaidensis* Mesn.(in part)(Fig. 51)

20'. Flagellomere 1 rounded distally along ventral margin; aristomere 3 average length (0.50-0.65 head height) 21

21(20'). Vibrissal angle with 3-6 setae and several setulae in addition to vibrissa and hairs; 3 postsutural dorsocentral setae; recorded from Washington and western Idaho (Fig. 88) . . . . *S. macronyx* n.sp.(Fig. 56)

21'. Vibrissal angle with 2-3 setae in addition to vibrissa and hairs; 3-4 postsutural dorsocentral setae 22

22(21'). Proboscis shorter than 2.3X head height; western USA 23

22'. Proboscis longer than 2.25X head height, or from central or eastern North America (*S. illinoiensis*). 24

[for specimens from western USA within or near overlap in proboscis length, check distribution maps and see "Remarks" under appropriate species]

23(22). Four postsutural dorsocentral setae; recorded from California and Washington (Fig. 87) . . . . *S. pacifica* n.sp.(Fig. 45)

23'. Three postsutural dorsocentral setae in most specimens; recorded from southwestern USA and Mexico (Fig. 83). . . . . *S. pisinnia* n.sp.(Fig. 49)

24(22'). Eye large (Fig. 54); proboscis shorter than 2.5X head height; central and eastern North America

(Fig. 92) . . . . . .*S. illinoiensis* (Tnsd.)(Fig. 54)

24'. Eye of average size (Figs. 46-47); proboscis longer than 2.25X head height; transcontinental (Figs. 93,95). . . . .*S. cristata* (Fabr.)(Fig. 46) . . . . .and *S. multifaria* n.sp.(Fig. 47) [see "Remarks" under *S. cristata* for discussion concerning separation of these species]

3.6.2 Key to adults of Siphona species of Middle America

1. Male. 2

1'. Female. . . . . 9 [female of *S. longissima* unknown]

2(1). Length of flagellomere 1: head height less than 0.52. 3

2'. Length of flagellomere 1: head height greater than 0.58, or not south of Tropic of Cancer (*S. multifaria*) 4

3(2). Preabdomen light coloured with narrow vitta; 3 postsutural (scutal) dorsocentral setae in all but a very few specimens; palpus yellow in most specimens, slightly infuscate apically in a few; distiphallus triangular and pointed in profile (Fig. 73); widely distributed, from central Mexico to Costa Rica (Fig. 96) . .*S. futilis* Wulp(Fig. 34)

3'. Preabdomen dark brown, not vittate, with narrow light coloured bands across anterior of T_3, T_4 and

T_5; 4 postsutural dorsocentral setae; palpus fuscous or black on apical half; distiphallus slender, apex truncate in profile (Fig. 74); Chiapas (Fig. 97) . . . . *S. brunnea* n.sp.(Fig. 35)

4(2'). Preabdomen broadly vittate (vitta wider than distance between median marginal setae on T_3), dark coloured; palpus infuscate apically; distiphallus short and broad in profile with small hooks along antero-ventral margin (Fig. 76); southern Mexico (Fig. 99) . . . .*S. akidnomyia* n.sp.(Fig. 36)

4'. Preabdomen average vittate (vitta not wider than distance between median marginal setae on T_3), light coloured; palpus yellow; distiphallus not shaped as above, with or without small hooks along antero-ventral margin 5

5(4'). Proboscis shorter than 2.3X head height; distiphallus slightly bent downward from basiphallus, shaped as in Fig. 65; southwestern USA to Mexico state, Mexico (Fig. 83) . . . .*S. pisinnia* n.sp.(Fig. 23)

5'. Proboscis longer than 2.6X head height, or if shorter (*S. multifaria*, 2.25-3.0X) then distiphallus sharply bent downward from basiphallus and not south of Tropic of Cancer 6

6(5'). North of Tropic of Cancer; distiphallus as in Fig.

67; widely distributed in Canada and USA (Fig. 93), presence in northern Mexico likely. . . . . *S. multifaria* n.sp.(Fig. 25)

6'. South of Tropic of Cancer 7

7(6'). Length of flagellomere 1: eye height less than 0.75; surstylus with apex extended slightly to far beyond apex of cerci (Fig. 79); distiphallus with apex rounded in profile; bend of R_1 bare; Veracruz (Fig. 98) . . . . *S. rizaba* n.sp.(Fig. 39)

7'. Length of flagellomere 1: eye height greater than 0.75; surstylus with apex even with or extended slightly beyond apex of cerci (Figs. 77-78); distiphallus with apex pointed in profile; bend of R_1 with single setula or bare 8

8(7'). Eye height greater than 0.86 head height; bend of R_1 with single setula on at least one side in most specimens; slope of distiphallus even with that of basiphallus; distiphallus dentate along antero-ventral margin (Fig. 78); Veracruz to Costa Rica (Fig. 101) . . . . *S. tropica* (Tnsd.)(Fig. 38)

8'. Eye height less than 0.85 head height; bend of R_1 bare; distiphallus bent sharply downward from angle of basiphallus; distiphallus with small hooks along antero-ventral margin (Fig. 77); Chiapas (Fig. 100) . . . . *S. longissima* n.sp.(Fig. 37)

9(1'). Proboscis longer than 2.7X head height. 10

9'. Proboscis shorter than 2.7X head height 12
[*S. multifaria* keys through both halves of couplet]

10(9). North of Tropic of Cancer; widely distributed in Canada and USA (Fig. 93), presence in northern Mexico likely . . . . *S. multifaria* n.sp.(in part)(Fig. 47)

10'. South of Tropic of Cancer 11

11(10'). Bend of R_1 with a single setula on at least one side in most specimens; Veracruz to Costa Rica (Fig. 101). . . . . *S. tropica* (Tnsd.)(Fig. 57)

11'. Bend of R_1 bare; Veracruz (Fig. 98) . . . .*S. rizaba* n.sp.(Fig. 58)
[male associates required for positive identification]

12(9'). Proboscis longer than 2.5X head height; wing brownish hyaline; southern Mexico (Fig. 99) . . . .*S. akidnomyia* n.sp.(Fig. 59)

12'. Proboscis shorter than 2.5X head height; wing yellowish or brownish hyaline 13

13(12'). Palpus with apical half fuscous or black; 4 postsutural dorsocentral setae; body dark brown; Chiapas (Fig. 97) . . . . *S. brunnea* n.sp.(Fig. 55)

13'. Palpus yellow; 3 postsutural dorsocentral setae in all but a very few specimens, or not south of

Tropic of Cancer; body blue-gray with brown areas, not extensively dark brown. 14

14(13'). Head profile as shown in Fig. 53; eye relatively large, flagellomere 1 relatively short; widely distributed, from central Mexico to Costa Rica (Fig. 96) . . . .*S. futilis* Wulp(Fig. 53)

14'. Head profiles as shown in Figs. 47,49; eye relatively small; flagellomere 1 relatively long. 15

15(14'). Proboscis shorter than 2.3X head height; southwestern USA to Mexico state, Mexico (Fig. 83) . . . .*S. pisinnia* n.sp.(Fig. 49)

15'. Proboscis longer than 2.25X head height; widely distributed in Canada and USA (Fig. 93), presence in northern Mexico likely . . . . *S. multifaria* n.sp.(in part)(Fig. 47)

3.7 The S. maculata group

This group is characterized by a short to very short proboscis and a slender flagellomere 1 broadly rounded apically along ventral margin. Weak lateral marginal setae on T_{1+2} are presumed symplesiotypic for the group, but this state is not expressed in all specimens (and not at all in *Siphona lurida*). There is a trend toward a smaller than average eye. Except for *Siphona pacifica*, adults are seen in spring and early summer.

3.7.1 Siphona maculata Staeger

Siphona maculata Staeger *in* Zetterstedt, 1849: 3212.-- Mesnil, 1965: 871 (redescription).

Recognition.-- Average-sized eye and flagellomere 1, very short proboscis. Most distinctive features are weak lateral marginal setae on T_{1+2} and small, well developed hooks on antero-ventral margin of distiphallus. Colouration of preabdomen average, vittate. Postsutural dorsocentral setae three.

Similar to *S. floridensis*, from which it can be separated by number of postsutural dorsocentrals, structure of distiphallus and geographical distribution.

Most easily confused with *S. intrudens*. Males are separated by structure of distiphallus. There are several trends which are useful for distinguishing between *S. intrudens* and *S. maculata*; these apply to both male and female specimens, though more conspicuous in former: *S. maculata* has a shorter proboscis, smaller tarsal claw, larger eye and longer flagellomere 1 than *S. intrudens*. With respect to females, preabdomen of most specimens of *S. intrudens* is black in ground colour overall, while preabdomen of *S. maculata* in most specimens has a short, broad vitta, with yellow ground colour laterally on T_{1+2} and antero-laterally on T_3.

Description.-- Specimens examined: 263 males, 117 females from North America; ca. 20 European specimens. *Length:* 3.5-5.0mm.

Male. *Head* (Fig. 18). *Colouration:* frontal vitta yellow to testaceous; gena and parafacial white to light yellow; frontal plate light yellow to light brown; scape and pedicel yellow to fuscous, flagellomere 1 in most specimens fuscous or black, testaceous in a few light coloured specimens; palpus yellow; proboscis reddish-brown to fuscous. *Eye:* size average for genus, 0.755-0.825 head height (Fig. 13), slender, widest at center, evenly rounded along anterior margin. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 0.564-0.640 head height (Fig. 14); length of aristomere 3 average for genus. *Mouthparts:* proboscis short, 1.30-1.74 head height (Fig. 15).

Thorax. Colouration: dorsum average, 3 brown vittae distinct in light coloured specimens, dorsum predominantly brown to dark brown in dark coloured specimens; tegula testaceous, light brown to brown; wing yellowish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, 44 specimens with three, 1 with four [males and females]. *Acropod:* claws and pulvilli average-sized.

Preabdomen. Colouration: faintly vittate; most specimens black in ground colour on T_4 and T_5 and medially on T_{1+2} and T_3, yellow in ground colour laterally on T_{1+2}

and T_3; areas black in ground colour with surface blue-gray or gray, dark brown or black around macrotrichial insertions, especially around median marginals on T_3 and T_4; areas yellow in ground colour with surface yellow to light brown; extent of black ground colour varied among specimens, in a few greater than average (posterior portion of T_3 black in ground colour) or less than average (anterior portion of T_4 yellow in ground colour). *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} weak, in most specimens scarcely or not at all differentiated from marginal hairs.

Genitalia (Fig. 60). Thirty-eight examined, including 2 from European specimens. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent sharply downward from angle of basiphallus; antero-ventral margin V-shaped in anterior view, armed with several well-developed hooks (though smaller than hooks on distiphallus of *S. intrudens*); in profile tapered to narrow apex.

Female. As described for male except as follows.

Head (Fig. 42). Palpus longer and thicker than in males in a few specimens.

Preabdomen. Colouration: very varied, most specimens darker than average male; average specimen yellow in ground colour laterally on T_{1+2} and antero-laterally on T_3, rest black in ground colour, dorsal vitta short and broad; range from entirely black in ground colour (vitta absent), to average condition described for male (vitta present); dark specimens with large dark brown or black areas around macrotrichial insertions.

Geographical distribution (Fig. 82).-- Europe and North America. Transcontinental in North America; most records within a rather narrow belt along southern limit of boreal forest.

Habitat.-- I have collected specimens of this species in mixed forest dominanted by maple (Gatineau Co., Que.) or aspen (Edmonton, Alta.). Individuals flew close to the ground in a zig zag pattern, apparently searching for ground-dwelling hosts.

Chorological affinities.-- *S. maculata* and *S. intrudens* are widely sympatric over much of their apparent ranges. A few examined series of specimens contain both *S. intrudens* and *S. maculata*, suggesting their ecological requirements are similar.

A closely related species, *S. floridensis*, is allopatric in distribution.

Phylogenetic relationships (Fig. 103).-- The phenetic similarity between *S. maculata* and *S. floridensis* suggests they might be sister species, though a synapotypy has not been found to substantiate this.

Of the North American taxa of the *S. maculata* group, only *S. maculata* and *S. intrudens* share the derived condition of hooks on the antero-ventral margin of the distiphallus (Figs. 60,62). However, on the basis of other characters, this condition is interpreted as derived at the base of the lineage terminating in *S. maculata*, *S. intrudens* and *S. lurida* (Fig. 103), precluding a sister group relationship between *S. maculata* and *S. intrudens*.

3.7.2 *Siphona floridensis* new species

Holotype.-- Male, labelled: "Orlando,/ Fla. [Florida, USA] III.3.[19]46/ F. Snyder" (AMHN). Terminalia in microvial on pin below specimen.

Allotype.-- Female, same data as holotype (AMNH).

Derivation of specific epithet.-- With only one record outside Florida, this species is named for its restricted known distribution.

Recognition.-- Average-sized eye and flagellomere 1, very short proboscis. Lateral marginal setae on T_{1+2} weak or strong. Distiphallus average in structure. Preabdomen vittate or black in ground colour overall. Postsutural dorsocentrals four.

Externally very similar to the allopatric *S. maculata*. The proboscis of both species is very short. *S. floridensis* has a slightly larger eye and slightly shorter flagellomere

1 than *S. maculata*. Males are separated by distiphallus structure (small hooks on antero-ventral margin in *S. maculata*) and number of postsutural dorsocentrals (three in *S. maculata*, four in *S. floridensis*).

Description.-- *Length:* 3.5-5.5mm.

Male. *Head* (Fig. 19). *Colouration:* as described for *S. maculata*. *Eye:* size average for genus, 0.783-0.839 head height (Fig. 13), broad, widest at center, evenly rounded along anterior margin. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 slightly shorter and thinner than in *S. maculata*, 0.548-0.574 head height (Fig. 14); length of aristomere 3 average for genus. *Mouthparts:* proboscis short, within range for *S. maculata*, 1.37-1.59 head height (Fig. 15).

Thorax. *Colouration:* dorsum average, 3 light brown vittae visible in most specimens, scutum and scutellum predominantly brown in a few specimens (generally somewhat lighter than in *S. maculata*); tegula testaceous; wing yellowish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, all specimens with four [males and females]. *Acropod:* claws and pulvilli average-sized.

Preabdomen. *Colouration:* specimens in "Orlando" series vittate, as described for average *S. maculata*; other males black in ground colour, surface light blue-gray or gray, dark brown to black around macrotrichial insertions. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} weak in 2 males and 4 females from "Orlando" series, strong in others.

Genitalia (Fig. 61). Four examined. Apex of surstylus extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent very slightly downward from angle of basiphallus in 3 specimens, bent more sharply (as in *S. maculata*) in one specimen; antero-ventral margin dentate (without hooks); apex broad in profile.

Female. As described for male except as follows.

Head (Fig. 43). Palpus longer and thicker than in males.

Preabdomen. Specimen from Lake Placid mottled black and yellow in ground colour, weakly vittate; other specimens black in ground colour, surface light blue-gray or gray.

Geographical distribution (Fig. 84).-- Known only from Florida and southern Georgia.

Chorological affinities.-- This is the only *Siphona* species restricted to extreme southeastern United States, and the only member of the *S. maculata* group recorded from that area. *S. multifaria* is the *Siphona* species known to be sympatric with this species.

Phylogenetic relationships (Fig. 103).-- This species is plesiotypic in almost all states, so its placement beyond species group cannot be clarified. It might be the sister species to *S. maculata*, as inferred from phenetic similarity and zoogeographic analysis.

Paratypes.-- Four males, 7 females. USA: *Florida:*Orlando, 3,15.III.46, F. Snyder, 2M, 4F; Wakulla Co., Ochlockonee R. St. Pk., 29.IV.70, W.W. Wirth, 1M; Highlands Co., Archbold Biological Station, 14.III.62, S.W. Frost, 1M; Archbold Biological Sta., L. Placid, 10.IV.66, R.W. Dawson, 1F; Biscayne Bay, 1F. *Georgia:* Liberty Co., St. Catherines Island, 24-28.IV.72, Thompson and Picchi, 1F. (Deposited in AMNH, PSU, USNM and WSUP.)

3.7.3 Siphona intrudens (Curran)

Bucentes intrudens Curran, 1932: 14.
Siphona intrudens: Sabrosky and Arnaud, 1965: 1064.

Type material examined.-- *Holotype*, male, labelled: "Bucentes/ intrudens/ Curran ♂ [red label]"; "Castle Rock/ IV-17-[19]08 Pa [Pennsylvania, USA] "Ac[cession]. 5642 A.J. Weidt coll."; "Bucentes/ intrudens/ Curran" (AMNH).

Allotype, female, same data as holotype except without fourth label (AMNH).

Recognition.-- Small to average-sized eye, average-sized flagellomere 1 and short proboscis. Most specimens with weak lateral marginal setae on T_{1+2}, large tarsal claws and a dark blue-gray preabdomen with dorsal vitta. A few specimens very similar to *S. maculata*, but

U-shaped distiphallus in anterior view with 3-4 large hooks along antero-ventral margin is unique to *S. intrudens*. Postsutural dorsocentrals three.

Can be confused with either *S. maculata* or *S. lurida*. For discussion concerning former, see "Recognition" under that species.

Specimens of *S. lurida* with a flagellomere 1 of average *Siphona* length are similar in general appearance to *S. intrudens*. The dark colouration of these species, with blue-gray, non-vittate preabdomens, contributes to their similarity and with other characteristics attests to their close phylogenetic relationship.

S. intrudens specimens with strong lateral marginals on T_{1+2} can be separated from *S. lurida* by the larger eye, presence of only 2-3 setae on vibrissal angle (besides vibrissa) and by the unique structure of the distiphallus.

Description.-- Specimens examined: 408 males, 338 females. *Length:* 3.5-5.5mm.

Male. *Head* (Fig. 20). *Colouration:* as described for *S. maculata*. *Eye:* small to average for genus, 0.703-0.817 head height (Fig. 13), slender, widest at center, evenly rounded along anterior margin. *Macrotrichia:* vibrissal angle with 2 or 3 setae and several hairs, setae in most specimens 2 in number, 1 laterad or above vibrissa and 1 below. *Antenna:* flagellomere 1 0.474-0.593 head height (Fig. 14); length of aristomere 3 average for genus. *Mouthparts:* proboscis short, 1.45-2.00 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray to blue with varied amounts of brown; 3 brown vittae not clearly differentiated in most specimens (*S. intrudens* generally with more blue on dorsum than *S. maculata*, and darker than *S. floridensis*); tegula testaceous to fuscous; wing yellowish to cinereous hyaline; legs average to darker than average, femur of hindleg predominantly reddish-brown in a few specimens. *Macrotrichia:* postsutural dorsocentrals, 68 specimens examined, all with three [males and females]. *Acropod:* claws and pulvilli large in most specimens (Fig. 5), average in a few.

Preabdomen (Fig. 7). *Colouration:* very varied, from black in ground colour, surface predominantly blue-gray or gray, to vittate condition described for *S. maculata*; most specimens from western North America dark form, both dark and light (vittate) forms well-represented in examined material from prairies to eastern North America. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} in most specimens weak, slightly stronger than surrounding hairs, in a few specimens not differentiated, in a few strong.

Genitalia (Fig. 62). Thirty-seven examined. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent sharply downward from angle of basiphallus; antero-ventral margin U-shaped in anterior view, with several large, well developed hooks (larger than in *S. maculata*); in profile tapered to narrow apex.

Female. As described for male except as follows.

Head (Fig. 44). Palpus longer and thicker than in males in most specimens.

Preabdomen. Colouration: most specimens black in ground colour, surface predominantly blue-gray or gray; a few specimens vittate, as described for average specimen of female *S. maculata*.

Geographical distribution (Fig. 85).-- Transcontinental species, records mostly south of boreal forest; particularly well recorded from northeastern United States.

Chorological affinities.-- Among *S. maculata* group members, this species is evidently parapatric or narrowly sympatric with *S. lurida* and *S. pacifica*. Also see notes under *S. maculata*.

Phylogenetic relationships (Fig. 103).-- This is a highly derived species, closely related to *S. lurida*. A decision on whether these species are sister species awaits a cladistic analysis of related (undescribed) Oriental species of *Siphona*.

See also notes under *S. maculata*.

3.7.4 Siphona lurida Reinhard

Siphona lurida Reinhard, 1943: 20.-- Sabrosky and Arnaud, 1965: 1064.

Type material examined.-- *Holotype*, male, labelled [lines not recorded]: "Rainier, Ore. [Oregon, USA] III.3.[19]30"; R.E. Dimick Coll."; "HOLOTYPE Siphona lurida Reinhard [red label]"; "Siphona lurida Rnh R'43 [Reinhard det. label]" (CNC).

Allotype, female [abdomen missing], labelled: "Union Hills/ II-20-1940/ R.E. Rieder, col."; ALLOTYPE/ Siphona/ lurida/ Reinhard [red label]"; "Siphona/ lurida/ Rnh. R. [Reinhard det. label]"; "PARATYPE/ Siphona/ lurida/ Reinhard [yellow label]" (FSCA).

Paratypes, 4 males, top two labels: "Union Hills/ Marion Co[unty]. Ore. [Oregon, USA]/ II-20-1940/ R.E. Rieder, col."; Paratype/ Siphona/ lurida/ Reinhard [red label]" (2 in CNC, 1 each in FSCA, OSU).

Recognition.-- Eye smaller than any other species, flagellomere 1 long in most specimens. Proboscis short. Cluster of 5-10 setae on vibrissal angle besides vibrissa and hairs, and above average number of hairs on parafacial and frontal plate (up to ca. 15). Dark coloured species, preabdomen black in ground colour overall, apex of palpus infuscate in most specimens. Tarsal claws large in most specimens. Wing cinereous hyaline. Lateral marginal setae on T_{1+2} strong. Postsutural dorsocentrals three. Adults are seen in very early spring to mid-summer; one southern record from December.

A few specimens are very similar to *S. intrudens*, as discussed under "Recognition" of that species.

S. lurida specimens with a very small eye and large flagellomere 1 are unmistakable. The holotype and paratypes are of this form, as are examined specimens of *S. lurida* from Japan. It is uncertain how prevalent are specimens with a short flagellomere 1, for the species has been inadequately collected.

Description.-- Specimens examined: 11 males, 9 females from North America; 1 male, 2 females from Japan. *Length:* 4.5-5.5mm.

Male. *Head* (Fig. 21). *Colouration:* frontal vitta bright orange to reddish-brown; gena and lower parafacial orange or yellow to gray, upper parafacial and frontal plate yellow or blue-gray to brown; orbital plate light to dark brown; scape, pedicel and a portion of flagellomere 1 above aristal insertion orange to fuscous, rest of flagellomere 1 fuscous to black; palpus yellow, apex infuscate in most specimens; proboscis reddish-brown to fuscous. *Eye:* very small, 0.627-0.677 head height (Fig. 13), slender, widest at center, evenly rounded along anterior margin. *Macrotrichia:* number and length of hairs on upper parafacial and fronto-orbital plate above average for genus in most specimens, up to 15 present; vibrissal angle with tight cluster of 5-10 setae and several hairs in addition to vibrissa. *Antenna:* flagellomere 1 very varied in length, 0.508-0.677 head height (Fig. 14); length of aristomere 3 average for genus. *Mouthparts:* proboscis short, 1.45-2.00 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or blue with 3 clearly differentiated brown vittae in most specimens, a few specimens with dorsum predominantly brown (very close to *S. intrudens*); tegula fuscous; wing cinereous hyaline; legs average to darker than average, femur of foreleg predominantly reddish-brown in a few specimens. *Macrotrichia:* postsutural dorsocentrals, 20 specimens examined, all with three [males and females]. *Acropod:* claws and pulvilli large in most specimens, average in a few.

Preabdomen. Colouration: not vittate; black in ground colour, surface varied, from predominantly blue-gray to predominantly dark brown mixed with black with blue-gray restricted to bands on anterior third of T_3, T_4, and T_5; dark brown or black around macrotrichial insertions. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 63). Six examined, including one from a Japanese specimen. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent sharply downward from angle of basiphallus; antero-ventral margin V-shaped in anterior view, dentate; in profile tapered to rounded apex.

Female. As described for male except as follows.

Head (Fig. 41). Palpus longer and thicker than in males in most specimens.

Preabdomen. *Colouration:* black in ground colour; surface varied, from predominantly blue-gray or gray to predominantly dark brown with or without narrow bands of blue-gray on anterior margins of T_3, T_4, and T_5.

Geographical distribution (Fig. 86).-- Japan (new record) and western United States.

Chorological affinities.-- In North America, this species is apparently parapatric or narrowly sympatric with *S. maculata* and closely related *S. intrudens*. The range of *S. pacifica* coincides with that of another *S. maculata* group member, *S. lurida*.

Phylogenetic relationships (Fig. 103).-- Like *S. intrudens*, this species is highly derived. It might be sister species to *S. intrudens*, as mentioned under that species.

3.7.5 *Siphona pacifica* new species

Holotype.-- Male, labelled: "Dartford, WASH. [Washington, USA]/ Malaise trap"; "R.D. Gray/ VI.10-11 1969"

(WSUP).

Allotype.-- Female, labelled: "Dartford, Wash/ VII-5-1970"; "Malaise trap/ R.D. Gray" (WSUP).

Derivation of specific epithet.-- This species is named after its western distribution.

Recognition.-- Proboscis length and eye height average, flagellomere 1 short. Preabdomen light blue-gray or gray, with or without dorsal vitta. Lateral marginal setae on T_{1+2} weak or strong. Distiphallus bent slightly downward from angle of basiphallus, apex broad in profile. Postsutural dorsocentral setae four.

This species has a unique set of characteristics that distinguish it from other species. However, taken singly these features are unremarkable, and *S. pacifica* is therefore difficult to recognize. It is placed in the *maculata* group because the flagellomere 1 is slender and broadly rounded apically along ventral margin, lateral marginal setae on T_{1+2} are weak in some specimens, and general colouration is typical of the group.

Description.-- *Length:* 3.5-5.0mm.

Male. *Head* (Fig. 22). *Colouration:* frontal vitta orange, testaceous to reddish-brown; gena and parafacial white, light yellow to light brown; fronto-orbital plate light brown to brown; scape and pedicel and in a few specimens a portion of flagellomere 1 above aristal insertion yellow; flagellomere 1 fuscous to black; palpus yellow; proboscis reddish-brown. *Eye:* size average to large for genus, 0.796-0.850 head height (Fig. 13), broad, widest at center, evenly rounded along anterior margin. *Macrotrichia:* vibrissal angle with 1 seta above vibrissa (or laterad) and in most specimens 2 setae below, and several short hairs. *Antenna:* flagellomere 1 short, 0.431-0.472 head height (Fig. 14); length of aristomere 3 average for genus. *Mouthparts:* proboscis length average for genus, 1.87-2.15 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or gray finely mixed with brown in most specimens, 3 brown vittae visible in most specimens; tegula testaceous; wing yellowish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, four in all specimens. *Acropod:* claws and pulvilli average-sized.

Preabdomen. Colouration: varied, vittate in a few specimens; most specimens predominantly or entirely black in ground colour, a few specimens with yellow ground colour laterally on T_{1+2} and T_3 or less; surface light coloured, areas of black ground colour light blue-gray or gray in surface colour, brown to black around macrotrichial insertions; areas yellow in ground colour with surface yellow or light brown. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} differentiated from marginal hairs, weak or strong.

Genitalia (Fig. 64). Two examined. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent slightly downward from angle of basiphallus; antero-ventral margin dentate; in profile anterior edge straight, apex broad.

Female. As described for male except as follows.

Head (Fig. 45). Length of palpus slightly longer than in males.

Preabdomen. Colouration: not vittate; black in ground colour, surface blue-gray or gray.

Geographical distribution (Fig. 87).-- Recorded from several localities in California and one in Washington.

Chorological affinities.-- The western distribution of this species is very similar to that of *S. lurida*. Two other species of the *S. maculata* group, *S. maculata* and *S. intrudens*, are evidently parapatric or narrowly sympatric with this species.

Phylogenetic relationships (Fig. 103).-- *S. pacifica* is interpreted as distantly related to most other North American members of the *S. maculata* group. This species possesses the synapotypic feature of the group - a slender, pointed fagellomere 1 - as well as the symplesiotypies, weak lateral marginal setae on T_{1+2} and a relatively short proboscis.

Paratypes.-- Seven males, 4 females. USA: *California:* Sugar Loaf Mt., 28.V.46, J. Sperry, 1M; Marin Co., Mill Valley, IX.51, E.S. Ross, 1M; Placer Co., Brockway, VII.41, G.E. Bohart, 1M. *Washington:* Spokane Co., Dartford, 6-9, 20-31.VI, 2-3.VII, 2-3.VIII.69, 5.VII.70, R.D. Gray, 4M, 3F; ibid., 23.VI.70, 1F. (Deposited in CAS, USNM and WSUP.)

3.8 The S. cristata group

Characteristics varied; most species with an average to long proboscis, average-sized eye, broad flagellomere 1 rounded or slightly truncate apically along ventral margin (not distinctly pointed), and an anterior indentation on the distiphallus. The three predominantly to entirely yellow North American *Siphona* species belong to this group.

3.8.1 Siphona cristata (Fabricius)

Stomoxys cristata Fabricius, 1805: 281.
Siphona cristata: Mesnil, 1964: 861 (redescription).--
Curran, 1932: 13 (in key; probable misidentification).
Siphona chaetolyga Rondani, 1865: 194.-- Herting, 1969: 192.
Siphona palpina Zetterstedt, 1859: 6064.-- Mesnil, 1964: 861.

Mesnil (1964) and Crosskey (1976b) followed earlier authors and listed *Siphona oculata* Pandellé as a synonym of

S. cristata. Herting recently examined the type of *S. oculata* and found it conspecific with *Siphona pauciseta* Rondani (Herting, 1978: 6).

My interpretation of this species is based on Mesnil's description (1964) and specimens determined by Drs. Mesnil and Herting.

Recognition.-- Eye height and flagellomere 1 length average, proboscis longer than average. Colouration very varied; in a few specimens thoracic pleura yellow in ground colour, dorsum dark in ground colour, rest of specimens with thorax predominantly dark in ground colour. Preabdomen of both sexes varied, from entirely yellow, to yellow with narrow median vitta, to average vittate with predominantly tawny surface colour. A very few specimens with 1 or 1 pair median marginal setae on T_{1+2} (3% each). Distiphallus bent sharply downward from angle of basiphallus, in most specimens with anterior edge curved inward ca. 0.33 of its length from ventral edge. Postsutural dorsocentral setae three (35%) or four (65%).

Due to varied nature of this species, identification can be difficult. A few specimens resemble *S. lutea* (as discussed under "Recognition" of that species), but do not pose a serious identification problem.

Separation of *S. cristata* and *S. pisinnia* is discussed under the latter species.

Specimens of *S. cristata* can be very difficult to separate from those of *S. multifaria*, for they are similar in most characteristics. Colouration is useful, but not always trustworthy. The yellow form of *S. cristata* is very distinct from *S. multifaria*, but specimens with vittate preabdomen are not always readily separable from *S. multifaria* specimens.

In Edmonton, Alberta, both species occur at the same time in the same place. *S. cristata* specimens are slightly larger and have a tawny, vittate preabdomen. The preabdomen of *S. multifaria* specimens has an indistinct light blue-gray vitta, is yellow laterally (not tawny as in *S. cristata*), and in most specimens has a very narrow brown pruinose vitta. Differences in distiphalli are recognizable, but do not hold for all specimens.

Since both *S. cristata* and *S. multifaria* are quite varied, the differences seen in Edmonton populations are not suitable for species discrimination in all areas. For this reason I have not separated these species in the key. Most male specimens should be identifiable on the basis of the foregoing remarks, though female specimens will not meet with equal success.

Description.-- Specimens examined: 78 males, 112 females from North America, ca. 10 European specimens. *Length:* 4.5-5.0mm.

Male. *Head* (Fig. 24). *Colouration:* as described for *S. lutea* except for antenna and proboscis; scape, pedicel and a portion of flagellomere 1 above aristal insertion yellow in most specimens, fuscous in a few; rest of flagellomere 1 testaceous to fuscous, in a few specimens black; proboscis brown to reddish-brown. *Eye:* size average to above average for genus, very varied, 0.754-0.855 head height (Fig. 13), slender to broad, widest at, or slightly above, center, narrowed or rounded below. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 0.547-0.672 head height (Fig. 14), resembling flagellomere 1 of *S. lutea* but more varied in length and shape; flagellomere 1 broad, varied from truncate to broadly rounded along ventral margin; length of aristomere 3 average for genus. *Mouthparts:* proboscis length above average for genus, very varied, 2.25-3.00 head height (Fig. 15).

Thorax. Colouration: black in ground colour in most specimens, light brown in ground colour on pleura in a few specimens; dorsum from yellow or light brown finely and evenly mixed with blue-gray or gray to entirely yellow, golden or brown; 3 brown or golden vittae dorsally in a very few specimens; tegula testaceous; wing yellowish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, 20 specimens with three, 37 with four [males and females]. *Acropod:* claws and pulvilli average in size.

Preabdomen. Colouration: one form predominantly yellow in ground colour, with or without narrow dark vitta, surface yellow to bright tawny; pattern varied from yellow form to average *Siphona* vittate form, with T_5, most of T_4, triangular area on T_3, and T_{1+2} medially black in ground colour, surface gray to brown; dark brown to black around macrotichial insertions; rest of preabdomen yellow in ground colour, surface yellow to tawny. *Macrotrichia:* most specimens without median marginals on T_{1+2}, a few with 1 seta on one side (6 specimens) or 1 pair (5 specimens); lateral marginals on T_{1+2} strong.

Genitalia (Fig. 66). Thirty-two examined, including 2 from European specimens. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent sharply downward from angle of basiphallus; antero-ventral margin dentate; in profile anterior edge varied, in most specimens indented ca. 0.33 distiphallus length from ventral edge, straight in a few specimens; apex broad in profile.

Female. As described for male except as follows.

Head (Fig. 46). Palpus longer and thicker than in males in most specimens.

Geographical distribution (Fig. 95).-- Wide ranging in Palearctic and Nearctic Regions, though sparsely recorded from latter over much of its apparent range.

Habitat.-- Ihave collected specimens of *S. cristata*, *S. lutea* and *S. multifaria* on flowers of the composite, *Erigeron philadelphicus* L., in river valley of the North Saskatchewan R., Edmonton, along shaded bank of a small stream in vicinity of poplar and scattered spruce.

Chorological affinities.-- In North America this wide ranging species is sympatric with closely related species *S. multifaria* and *S. lutea*, in addition to most other *Siphona* species of America north of Mexico. As noted above, specimens of *S. multifaria* and *S. lutea* have been caught in the same locality as those of *S. cristata*. In southwestern New Mexico, specimens of *S. pisinnia* were collected with specimens of this species.

Phylogenetic relationships (Fig. 104).-- Close to *S. multifaria* among North American species,though the sister species might be a Palearctic species.

3.8.2 Siphona multifaria new species

Holotype.-- Male, labelled: "MI. 87, Y.T. [Yukon Territory, Canada]/ Dempster Hwy./ 8-12.VII.1973/ G.&D.M. Wood" (CNC).

Allotype.-- Female, same data as holotype except date 16-17.VII.1973 (CNC).

Derivation of specific epithet.-- From the Latin *multifarius*, meaning "having great variety". *S. multifaria* is so named because it is a widely distributed species of varied appearance, being particularly difficult to identify because of its resemblance to *S. cristata*.

Recognition.-- Eye height and length of flagellomere 1 average, proboscis longer than average. Wing yellowish hyaline in most specimens, cinereous in a few. Male preabdomen varied, in most specimens light coloured, vittate, with a very narrow brown pruinose vitta (unassociated with vitta produced by ground colour), a few specimens predominantly black in ground colour. Female preabdomen darker than in male, not vittate. A very few specimens with 1 median marginal seta on one side on T_{1+2} (2%). Distiphallus bent sharply downward from basiphallus, anterior edge slightly or not at all curved inward ca. 0.33 of its length from ventral edge. Most specimens (65%) with three postsutural dorsocentral setae.

Most difficult to separate from *S. cristata*, as discussed under "Recognition" of that species.

S. multifaria and *S. pisinnia* are narrowly sympatric in southwestern United States. Specimens from that region should be checked carefully against data in the Hubbs-Hubbs diagrams, for colouration is essentially the same in both species, and differences between distiphalli are not diagnostic. The data base for *S. multifaria* and *S. pisinnia* is large enough that measurements cited in key, especially with reference to male specimens, should be representative of the two species.

Description.-- *Length:* 3.5-5.0mm.

Male. *Head* (Fig. 25). *Colouration:* frontal vitta orange or yellow to testaceous; gena and lower parafacial white to light yellow; upper parafacial and fronto-orbital plate light yellow to brown, darkest on orbital plate, in a few specimens fronto-orbital plate bright yellow (these specimens resembling *S. cristata*); scape, pedicel, and in a few specimens a portion of flagellomere 1 above aristal insertion yellow to testaceous, in a few specimens reddish-brown or fuscous; flagellomere 1 reddish-brown, fuscous or black; palpus yellow; proboscis light brown to reddish-brown or fuscous. *Eye:* size average to above average for genus, very varied, 0.755-0.854 head height (Fig. 13), slender, widest at center, evenly rounded along anterior margin. *Macrotrichia:* vibrissal angle with 2 or 3 setae and several hairs, setae in most specimens 2 in number (average for genus), 1 laterad or above vibrissa and 1 below. *Antenna:* flagellomere 1 very varied in length, 0.531-0.675 head height (Fig. 14); shape of flagellomere 1 varied, as described for *S. cristata*; length of aristomere 3 average for genus. *Mouthparts:* proboscis length above average for genus, very varied, 2.31-3.02 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or gray finely mixed with brown in most specimens, 3 brown vittae visible in a few specimens; tegula testaceous; wing yellowish hyaline in most specimens, cinereous hyaline in a few; legs average. *Macrotrichia:* postsutural dorsocentrals, 68 specimens with three, 37 with four [males and females]. *Acropod:* claws and pulvilli average-sized.

Preabdomen. Colouration: faintly or clearly vittate; most specimens black in ground colour on T_5, most or all of T_4, and medially on T_{1+2} and T_3, surface blue-gray, gray or light brownish-gray; dark brown to black around macrotrichial insertions; surface of most specimens with a faint or distinct narrow median brown pruinose vitta, narrower than vitta formed by black ground colour; areas yellow in ground colour with surface yellow or light brown; in a few specimens black ground colour more extensive, covering most of T_3, all of T_4 and T_5, with wide vitta T_{1+2}. *Macrotrichia:* most specimens without median marginals on T_{1+2}, 7 with 1 on one side (1 specimen from Labrador, 6 from western North America); lateral marginals on T_{1+2} strong.

Genitalia (Fig. 67). Fifty-six examined. As described for *S. cristata*, except anterior edge of distiphallus in profile straight or slightly indented in most specimens, very few specimens with indentation as strong as in average *S. cristata*.

Female. As described for male except as follows.

Head (Fig. 47). Palpus longer and thicker than in males in most specimens.

Preabdomen. Colouration: darker than male; most specimens not vittate, black in ground colour except laterally on T_{1+2}; surface blue-gray, mixed with brown, in a few specimens very light, in a few very dark.

Geographical distribution (Fig. 93).-- Very widely distributed throughout eastern and western North America; records absent for central plains.

Habitat.-- See *S. cristata*.

Chorological affinities.-- Due to the ubiquitous nature of this species, it is sympatric with all other *Siphona* species of America north of Mexico. Specimens of *S. cristata* and *S. lutea* have been caught together with those of this species.

Phylogenetic relationships (Fig. 104).-- Because this species is wide ranging in North America and recorded from northern localities, I consider its presence in the Palearctic Region likely. Therefore its sister species is not necessarily a species of Nearctic distribution. I regard *S. cristata* as the closest *Siphona* species to *S. multifaria* in North America.

Paratypes.-- One hundred and eigthy-nine males, 128 females. CANADA. *Alberta:* George L., 53°57'N 114°06'W, 13-17.VIII.66, P. Graham, 1M; Edmonton, 19.V.47, E.H. Strickland, 1F; ibid., 1932, O. Bryant, 1M; ibid., 29.VI.80, J.F. Landry, 2M; ibid., 7,8.VII.80, 30.VI, 3,6.VII.81, J.E. O'Hara, 13M; Mildred L., 57°03'N 111°35'W, 11-15.VII.79, J. Ryan and G. Hilchie, 1M; Banff, 3.VII.49, E.H. Strickland, 1F; Banff N.P., 8.VII.55, R. Coyles, 1M; Frank, 15.VI.62, W.R.M. Mason, 1M; Medicine Hat, 22.VI.74, J.F. McAlpine, 1M; Cypress Hills, 10.VIII.49, E.H. Strickland, 3F. *British Columbia:* Summit L., mi. 392, Alaska Hwy., 4500', 29-30.VI, 2-4,11-14.VII.59, R.E. Leech, 2M, 1F; ibid., 4200', 21,31.VII, 19-21.VIII.59, R.E. Leech, 6M, 1F; ibid., 19-21.VIII.59, E.E. MacDougall, 2F; Lakelse L. bog, s. of Terrace, 11,27.VI.60, B. Heming, 2M; ibid., 11.VII.60, C.H. Mann, 1M; Lac La Hache, 15.VII.73, H.J. Teskey, 1M; Keremeos, 18.VI.23, C.B. Garrett, 1M; Atlin, 2200', 3.VII.55, H.J. Huckel, 1M; Horsefly, 14.VII.73, H.J. Teskey, 1M; Ketchum L., 58°22'N 131°45'W, 3600', 23.VIII.60, W.W. Moss, 1F; ibid., R. Pilfrey, 2F; McQueen L., 10 mi. n. Kamloops, 2.VII.73, H.J. Teskey, 1F. *New Brunswick:* Kouchibouquac N.P., 10,24.VI.77, J.R. Vockeroth, 3M, 6F; ibid., 7.VII.77, J.F. McAlpine, 1M; St. Andrews, 3.VIII.57, G.E. Shewell, 1M. *Newfoundland:* St. John's, 21.VII.67, J.F. McAlpine, 1F; Cartwright, Labrador, 19.VII.55, E.E. Sterns, 1F. *Northwest Territories:* Norman Wells, 8,16.VIII.69, G.E. Shewell, 2F. *Ontario:* Maynooth, 9.VIII.74, D.M. Wood, 1M; Mer Bleu, 5 mi. e. Ottawa, 3,11.VI.66, D.D. Munroe, 2M; Mink L., nr. Maynooth, 27.VII.55, J.F. McAlpine, 1M; Forestry Station, Petawawa, 28.V.59, J.R. Vockeroth, 1M; Petawawa, 28.V.59, J.R. Vockeroth, 3F; Go Home Bay, 8 mi. w. Bala, 22.V.59, J.G. Chillcott, 1M; Foxboro, 10.V.63, A.F. Johnson, 1M. *Quebec:* Gatineau Co., Masham Twp., 25-31.VII.74, D.M. Wood, 2M; Lac Larouche, La Vérendrye Pk., 30.VII.72, D.M.

Wood, 2M, 2F; Mistassini Post, 18.VII.56, J.R. Lonsway, 1M; 4 mi. n. Eardley, 20,25.VIII.71, D.M. Wood, 1M, 3F; Kam. Co., Parke Reserve, 28.VII.57, G.E. Shewell, 1M; Duncan L., nr. Rupert, 28.VII, 9.VIII.70, 31.VII, 14.VIII.71, J.F. McAlpine, 3M, 2F. *Yukon Territory:* 14 mi. e. Dawson, 1300', 4.VIII.62, P.J. Skitsko, 1F; 17 km. wnw. Burwash Flats, 1250m, 10.VII.80, Wood and Lafontaine, 1F; mi. 40, Dempster Hwy., 1-6.VII.73, G. and D.M. Wood, 1M; mi. 87, Dempster Hwy., 27-30.VI, 1-12,18-27.VII, 4-8.VIII.73, G. and D.M. Wood, 37M, 23F; mi. 51, Dempster Hwy., 18-27.VII.73, G. and D.M. Wood, 1M; km. 140.5, Dempster Hwy., 900m, 27-29.VII, 1.VIII.80, Wood and Lafontaine, 1M, 7F; km. 155, Dempster Hwy., 950m, 29.VI-3.VII.80, Wood and Lafontaine, 2M, 3F.

USA: *Alabama:* Eufaula, 18.VI.54, R.L. Fischer, 1F. *Alaska:* Richard Hwy., Donnelly Dome, 25.VI.51, W.R.M. Mason, 1M; Cape Thompson, 1.VIII.61, R. Madge, 1F; Unalakleet, 17.VII, 11.VIII.61, B.S. Heming, 2F; Kodiak, IX.17, J.S. Hine, 1F; Douglas, 4.VIII.01, E. Jenne, 1F; Katmai, VIII.17, J.S. Hine, 1M; King Salmon, Naknek R., 10.VII, 10.VIII.52, W.R. Mason, 1M, 1F; ibid., 2-3.VIII.52, J.B. Hartley, 3F; Naknek, 18.VII, 8.VIII.52, W.R. Mason, 3F. *Arizona:* Sunnyside Canyon, Huachuca Mts., 9.VII.40, D.E. Hardy, 2F; Cochise Co., Southwestern Research Station, 8 km. w. Portal, 1650m, 21.VIII.62, 2M; ibid., 27.X.64, 1F; ibid., 3.XI.64, V.D. Roth, 1F; ibid., 14.VIII.65, 2M; ibid., 9.VII, 27.VIII.65, V.D. Roth, 2M; ibid., 5-25.IX.65, C.W. Sabrosky, 3M, 1F; ibid., 23.IX.66, P.H. Arnaud, Jr., 1M; ibid., 26.IX.66, V.D. Roth, 1F. *California:* Mono Co., Leavitt Meadow, 7200', 12.VIII.63, H.B. Leech, 1F; Trinity Co., Butter Creek, 3450', ca. 12 mi. se. Hyampom, 21,22.VII.68, H. Leech, 4M. *Colorado:* Mt. Evans, Doolittle Ranch, 9800', 22,23.VII, 3.VIII.61, J.G. Chillcott, 3M; ibid., 3.VIII.61, W.R.M. Mason, 4M, 1F; ibid., C.H. Mann, 1M; ibid., B.H. Poole, 1M, 1F; Mt. Evans, Echo L., 10,600', 12.VIII.61, C.H. Mann, 1F; Boulder, 1922, 1M; Pingree Pk., 17.VIII.32, 1F; Mesa Co., Glade Pk., 8.VII.53, Gurney, 1F. *Florida:* Inverness, Robertson, 1M; S. Florida, Robertson, 2M, 2F; Lake Co., Paisley, 18.II.66, C.L. Felshaw, 1M. *Georgia:* Dallas, 2.VI.40, P.W. Fattig, 1F; Lumpkin Co., 15mi. nw. Dahlonega, 25.VI.69, F. Santana, 1M; Oconee Co., 4mi. s. Farmington, 20.III.75, B.F. Freeman, 1M. *Idaho:* Newman L., 16.V.25, A.L. Melander, 1F; Viola, 26.VI.12, J.M. Aldrich, 1F. *Massachusetts:* Chester, 3.VIII, C.W. Johnson, 1M; Essex, 20.VII.11, 1F; Cuttyhunk Is. and Elisabeth Is., 21.VIII.71, C.T. Parsons, 1F. *Michigan:* Thayers, 16.V.55, J.R. Vockeroth, 1F; Montcalm Co., Flat River Game Area, 14.V.55, R. L. Fischer, 1M; Emmet Co., 27.V.60, R. and K. Dreisbach, 6M; Charlevoix Co., 31.V.60, R. and K. Dreisbach, 3M, 1F; Iron Co., 26.VIII.59, R. and K. Dreisbach, 1M; Hillsdale Co., 21.V.60, R. and K. Dreisbach, 1M, 2F; Saginaw Co., 24.V.60, R.R. Dreisbach, 1M. *Montana:* Granite Co., Elkhorn Ranch, 9 mi. s. Clinton, 3800', 26.VI.71, J.R. Powers, 1M. *New Hampshire:* Flume, n. Woodstock, 19.VII.35, Blanton and Borders, 1F; Franconia, 1M; Halfway House, to Gorham, 20.VII.35, Blanton and Borders, 1M; Gorham, 19.VIII.56, W.A. Drew, 1F; ibid., R.W. Hodges, 1M; ibid., 14.VIII.58, J.R. Vockeroth, 1M. *New Jersey:* Avalon, 8.VI, 2M; ibid., 30.VI, 1F. *New York:* Lake Placid, 2000', 19.VII.62, J.R. Vockeroth, 3M, 1F; ibid., J.G. Chillcott. 3M, 1F; Keene Valley, 10.VIII.16, E.L. Diven, 1M, 1F; Dug Mt., 8.VIII.12, D.B. Young, 1M; Olean, 5.IX.13, 1F; Babylon, L.I., 9.VI.35, 28.VIII.36, Blanton and Borders, 8M, 12F; ibid., 5.VIII.37, F.S. Blanton, 1F. *North Carolina:* Highlands, 3-5000', IV.36, R.C. Shannon, 1M; ibid., 3800', 29.V.57, J.R. Vockeroth, 1F; Cumberland Co., Fort Bragg, 16.V, 27.IX-3.X.67, J.D. Birchim, 1M, 1F. *Oregon:* Deschutes Co., Meadow Cpgd., Bend, 3840', 29.VII.70, P.H. Arnaud, Jr., 1M. *Pennyslvania:* West Co., Pitcairn, 17.V.65, J.G. Chillcott, 1M. *Tennessee:* Gatlinburg, 22.VI.40, R.C. Osburn, 1M. *Utah:* Grand Co., Warner Ranger Station, 28 mi. ese. Moab, 9200', 2.VIII.60, F., P. and B. Rindge, 1M. *Vermont:* Chittenden, Rutland, 1-15.VIII.16, J. Bequaert, 3M; Norwich, 7.VII, C.W. Johnson, 1F. *Washington:* Glacier Pk., Avalanche L., 14.VII.35, A.L. Melander, 1M; Asotin Co., Fields' Spr. St. Pk., 15.VI.72, W.J. Turner, 1M; Yakima Co., 8 mi. sw. Tieton R.S., Bear Creek, 16,28.VII.72, W.J. Turner and W.B. Garnett, 7M. *Wisconsin:* Polk Co., VII, Baker, 1F. *Wyoming:* Sweetwater Co., (Old) Hwy. 187, 11.5 mi. s. Eden, 23.VIII.65, H.B. Leech, 1M. (Deposited in AMNH, CAS, CNC, CUI, FSCA, INHS, JEOH, MCZ, MSU, OUCO, UASM, UGA, UGG, UKL, USNM, and WSUP.)

3.8.3 Siphona lutea (Townsend)

Crocuta lutea Townsend, 1919: 584.

Siphona lutea: Sabrosky and Arnaud, 1965: 1064.

Siphona tenuis Curran, 1933: 10.-- Sabrosky and Arnaud, 1965: 1064. **New synonymy.**

Notes about synonymy.-- Curran did not include *S. lutea* (Townsend) in his 1933 key to adults of North American *Siphona* species. This suggests he was unaware of Townsend's description of this species when he described *S. tenuis* in 1933. I have examined the types of both nominal species and regard them conspecific.

Type material examined.-- *Crocuta lutea* Townsend, 1 syntype[4], herein designated LECTOTYPE, female, labelled: "TD 4518 [handprinted]"; "Franconia/ NH [New Hampshire, USA]"; "20.VII,[19]15"; CHT Townsend/ coll" (USNM). My lectotype label "LECTOTYPE/ Crocuta/ lutea Tnsd./ O'Hara designation/ Selected 1981 [red bordered label]" has been attached to this specimen.

Siphona tenuis Curran, HOLOTYPE, male [left wing, 4 legs missing], labelled: "Siphona/ tenuis/ Curran ♂ [red type label]"; "Timagami, Ont. [Ontario, Canada]/ 1.VIII.1932/ A.W.A. Brown"; "Siphona/ tenuis/ Curran"

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[4] Townsend described *S. lutea* from 2 specimens; specimen examined does not bear red "USNM Type" label like other specimen in USNM (Sabrosky, per. comm.), but its locality and date labels signify it is the second syntype.

(AMNH).

Recognition.-- Particularly distinct because of yellow ground and surface colour overall. Most specimens examined (78%) with R_{4+5} setulose beyond crossvein r-m on at least one side. Similarly, R_1 distally with 1-2 setulae on at least one side in half the specimens (53%). Most specimens (94%) with four postsutural dorsocentral setae.

Shares with *S. oligomyia* the synapotypic character state of yellow ground and surface colouration. Differs from *S. oligomyia* in possessing a shorter proboscis and four postsutural dorsocentrals and lacking a modified male sternum 5.

The only other species resembling *S. lutea* is *S. cristata*. The preabdomen of most specimens of *S. cristata* is yellow with a thin dark median vitta; in a few specimens it is darker, or entirely yellow as in *S. lutea*. The darker thorax of *S. cristata* serves to separate specimens of that species from *S. lutea* where abdominal colouration is ambiguous. Also, most specimens of *S. lutea* are setulose on R_{4+5} beyond crossvein r-m, unlike other North American species.

Description.-- Specimens examined: 41 males, 39 females. *Length:* 4.0-5.5mm.

Male. *Head* (Fig. 26). *Colouration:* frontal vitta orange or yellow to testaceous; gena and parafacial white to yellow; fronto-orbital plate yellow, bright yellow to gold;

scape, pedicel, palpus and proboscis yellow; flagellomere 1 yellow to testaceous. *Eye:* size average for genus, 0.760-0.821 head height (Fig. 13), slender, widest at center, in most specimens evenly rounded along anterior margin, in a few slightly narrowed below center. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 0.561-0.643 head height (Fig. 14), broad and slightly truncate; length of aristomere 3 average for genus. *Mouthparts:* proboscis slightly shorter than average for genus, 1.83-2.14 head height (Fig. 15).

Thorax. Colouration: yellow in ground colour and pruinosity; tegula yellow; wing yellowish hyaline; femora and tibiae yellow. *Macrotrichia:* postsutural dorsocentrals, 2 specimens with three, 31 specimens with four [males and females]; wing, 32 males and females examined, R_{4+5} setulose beyond crossvein r-m on at least one side in 25 specimens, R_1 with at least 1 setula on apical third on at least one side in 17 specimens, CuA_1 with 1 to 3 setulae in 4 specimens. *Acropod:* claws and pulvilli average-sized (Fig. 6).

Preabdomen. Colouration: yellow in ground and surface colour; a few specimens with red or dark areas posteriorly where dark coloured internal structures are visible through translucent exoskeleton. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 68). Nine examined. Apex of surstylus extended slightly beyond apex of cerci. *Aedeagus:*

distiphallus bent sharply downward from angle of basiphallus in most specimens; antero-ventral margin dentate; in profile anterior edge slightly indented ca. 0.33 distiphallus length from ventral edge in most specimens, straight in a few; apex broad or narrow in profile. *Sternum 5* (Fig. 10): average for genus.

Female. As described for male except as follows.

Head (Fig. 48). Palpus longer and thicker than in males in most specimens.

Geographical distribution (Fig. 89).-- Transcontinental, in narrow belt south of boreal forest.

Habitat.-- Label data indicates specimens of this species have been collected from sphagnum bogs. Also see *S. cristata*.

Chorological affinities.-- This species is evidently parapatric with sister species *S. oligomyia*. The range of this species is broadly sympatric with ranges of closely related *S. cristata* and *S. multifaria*, as well as with ranges of *S. hokkaidensis*, *S. maculata*, *S. intrudens* and *S. medialis*.

Phylogenetic relationships (Fig. 104).-- This species and *S. oligomyia* are interpreted as sister species on the basis of their highly derived colouration and setula on bend of R_1. Together I interpret these species as the sister lineage to the *S. cristata - S. multifaria* lineage.

3.8.4 Siphona oligomyia new species

Holotype.-- Male, labelled: "Keremeos, B.C. [British Columbia, Canada]/ 20.VI 1923/ C.B. Garrett" (CNC). Terminalia in microvial on pin below specimen.

Derivation of specific epithet.-- Formed from *oligos* and *myia*, Greek for "few" and "fly" respectively. This combination was chosen because the type-series is comprised of but two specimens, collected over 1000 kilometers apart.

Recognition.-- Yellow ground and surface colour as in *S. lutea*. This is the only North American species with antero-lateral arms of sternum 5 hooked inward. R_1 distally with one setula on only one side in both specimens. Postsutural dorsocentral setae three. Female of species unknown.

This species is compared with *S. lutea* under "Recognition" of that species.

The characterization of *S. oligomyia* remains incomplete until more specimens are collected and examined and female of the species recognized. In particular, usefulness of proboscis length as a means for distinguishing *S. oligomyia* from *S. lutea* needs testing, and wing setular characteristics require additional data to establish trends.

Description.-- *Length:* 4.0-4.5mm.

Male. *Head* (Fig. 27). *Colouration:* as described for *S. lutea*. *Eye:* size average for genus though smaller than eye of *S. lutea*, 0.741-0.750 head height (Fig. 13), slender, widest at center, evenly rounded along anterior margin. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 0.574-0.596 head height (Fig. 14), broadly rounded distally along ventral margin; length of aristomere 3 average for genus. *Mouthparts:* proboscis longer than in *S. lutea*, average for genus, 2.30-2.35 head height (Fig. 15).

Thorax. *Colouration:* yellow in ground colour and pruinosity; tegula yellow; wing yellowish hyaline; femora and tibiae yellow. *Macrotrichia:* postsutural dorsocentrals, both specimens with three; wing: R_{4+5} not setulose beyond crossvein r-m (ie. average, cf. *S. lutea*); R_1 with single setula on apical third on one wing only in both specimens. *Acropod:* claws and pulvilli slightly larger than average.

Preabdomen. *Colouration:* yellow in ground and surface colour. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 69). Both holotype and paratype examined. Apex of surstylus ca. even with apex of cerci. *Aedeagus:* distiphallus slightly bent downward from angle of basiphallus; antero-ventral margin dentate; in profile anterior edge convex, not indented (as it is in most *S. lutea*); apex broad in profile. *Sternum 5* (Fig. 11): antero-lateral margins hooked inward.

Female. Unknown.

Geographical distribution (Fig. 90).-- Known only from Lake Tahoe, Calif., and Keremeos, B.C.

Chorological affinities.-- Though this species has been inadequately collected, it is apparently parapatric with sister species *S. lutea*. Among other *S. cristata* group members, it is sympatric with *S. cristata* and *S. multifaria*. Similar in distribution are *S. lurida* and *S. pacifica* of the *S. maculata* group.

Phylogenetic relationships (Fig. 104).-- This species is sister species to *S. lutea*, as mentioned under that species.

S. cuthbertsoni Curran (described from Salisbury, Zimbabewe) and *Siphonopsis* species have the antero-lateral arms of male sternum 5 hooked inward, as in *S. oligomyia*. *S. oligomyia* is not closely related to *S. cuthbertsoni*, and neither is closely related to *Siphonopsis* species.

Paratype. One male. USA: *California:* Lake Tahoe, 20.VI.15, A.K. Fisher (USNM).

3.8.5 Siphona pisinnia new species

Holotype.-- Male, labelled: "USA N.M. [New Mexico] Grant Co./ Gila Nat. For. Cherry/ Ck. Campgrd. 21km.n./ Silver City 2250m./ 3-4.VIII.1980/ J.E. & W.M. O'Hara"

(CNC).

Allotype.-- Female, same data as holotype (CNC).

Derivation of specific epithet.-- To my knowledge "pisinnia" has no classical meaning, and was chosen as an arbitrary combination of letters.

Recognition.-- Eye height and proboscis length average, flagellomere 1 long and broad in most specimens (the most distinctive external feature). Male preabdomen light coloured, faintly vittate. Female preabdomen darker, not vittate. Distiphallus slightly bent downward from angle of basiphallus, shape not very distinctive; anterior edge straight or slightly rounded, apex broad or narrow in profile. Postsutural dorsocentral setae three in most specimens (87%).

In Mexico male and female specimens are easily distinguished by head characteristics. Male genitalia of *S. pisinnia* are quite different from those of Mexican species.

In southwestern United States *S. cristata* specimens have been caught with specimens of *S. pisinnia*. Differences in colouration, eye size, flagellomere 1 and proboscis lengths will in most instances separate specimens of these species. Most *S. cristata* specimens are slightly larger than those of *S. pisinnia*.

Very similar to *S. pisinnia* is *S. multifaria*. Differentiation between the two is discussed under

"Recognition" of *S. multifaria*.

Description.-- *Length:* 3.0-5.0mm.

Male. *Head* (Fig. 23). *Colouration:* frontal vitta yellow to brown or reddish-brown; gena and lower parafacial white to light yellow; upper parafacial and fronto-orbital plate light yellow to brown, darkest on orbital plate; scape and pedicel testaceous to fuscous; flagellomere 1 fuscous to black; palpus yellow; proboscis reddish-brown or fuscous. *Eye:* size average for genus, 0.725-0.811 head height (Fig. 13), slender, widest at center, evenly rounded along anterior margin. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 very varied, in most specimens long and broad, 0.577-0.740 head height (Fig. 14), in most specimens rounded distally along ventral margin, in a few specimens slightly truncate; length of aristomere 3 average for genus. *Mouthparts:* proboscis length average for genus, 1.87-2.32 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or gray, finely mixed with brown in most specimens, 3 brown vittae visible in a few specimens; tegula testaceous to fuscous; wing yellowish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, 53 specimens with three, 8 with four [males and females]. *Acropod:* claws and pulvilli average-sized.

Preabdomen. Colouration: faintly vittate; most specimens black in ground colour on T_3, T_4 and medially on

T_{1+2} and T_3, rest of preabdomen yellow in ground colour; surface blue-gray, gray or light brownish-gray on areas of black ground colour, dark brown to black around macrotrichial insertions; areas yellow in ground colour with surface yellow or light brown; in a few specimens black ground colour extensive, covering most of T_3, all of T_4 and T_5, with broad vitta on T_{1+2}.

Genitalia (Fig. 65). Thirteen examined. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus slightly bent downward from angle of basiphallus; antero-ventral margin dentate; in profile anterior edge straight or slightly rounded; apex broad or narrow in profile.

Female. As described for male except as follows.

Head (Fig. 49). Palpus longer and thicker than in males in most specimens.

Preabdomen. Colouration: darker than male, not vittate; black in ground colour in most specimens, yellow laterally on T_{1+2} in a few specimens; surface blue-gray or gray, mixed with light brown.

Geographical distribution (Fig. 83).-- A western species, ranging from southwestern United States to central Mexico.

Habitat.-- I have collected specimens from one locality each in western New Mexico and eastern Arizona. At the former, in pine-juniper zone, a large series was collected from flowers of a short geranium (unidentified), while a few specimens were caught on white sweet clover (*Melilotus alba*). In eastern Arizona, in pine-spruce zone, specimens were swept from grass under cover of pine trees.

Chorological affinities.-- Uniquely distributed throughout southwestern United States and western Mexico, this species is narrowly sympatric with *S. multifaria* and *S. cristata* along the northern limit of its range. It is allopatric to other *S. cristata* group members.

Phylogenetic relationships (Fig. 104).-- Though not well characterized, the *S. cristata* group is considered monophyletic, and *S. pisinnia* is tentatively regarded as sister species to the other members of the group. Phenetically, *S. pisinnia* is close to *S. multifaria*.

Paratypes.-- Sixty-eight males, 73 females. USA: *Arizona:* Rustler Pk., Portal, 8200', 3.VIII.55, R.R. Dreisbach, 1M; Santa Catalina Mts., 14.VII.50, L.D. Beamer, 1M; Dripping Springs, Organ Pipe, 31.III.67, D.M. Wood, 1M; Sunnyside Canyon, 11.VII.40, D.G. Hall, 1M; ibid., Huachuca Mts., 9.VII.40, E.E. Kenaga, 1F; ibid., D.E. Hardy, 2F; Chiricahua Mts., 6.VIII.33, Bryant, 1M; ibid., 7.VIII.41, R.H. Beamer, 1M; Cochise Co., Chiricahua Mts., Flys Peak, 85-9700', 5.VIII.27, J.A. Kusche, 1M; Cochise Co., Southwestern Research Station, 8 km. w. Portal, 1650m, 13.VII.56, E. Ordway, 1M; ibid., 3.IX.59, D.D. Linsdale, 1M; ibid., 9,22.X.64, P.H. Arnaud, Jr., 3F; ibid., 27.VII.65, 1M; ibid., 2.VIII.65, 1F; ibid., 22.IX.65, 1F; ibid., 2.X.65, 1F; ibid., 5-25.IX.65, C.W. Sabrosky, 2M, 13F; ibid., 6.VIII.65, 8,26.IX.66, V.D. Roth, 1M, 9F; ibid., 11,19,22,24.IX.66, P.H. Arnaud, Jr., 1M, 11F. *California:* Snow Creek, 1500', 7.III.55, W.R. Richards, 1F; Garnet, 4.IV.45, A.L. Melander, 1F; Indio, 13.XII.44, A.L. Melander, 2F; nr. Indio, 23.II.49, A.L. Melander, 1M; Riverside, 2.V.35, A.L. Melander, 1M; Riverside Co., Deep Canyon, 23.II.64, M.E. Irwin, 1F; ibid., P.L. Boyd Desert Research Center, s. Palm Desert, 16-17.X, 4-6.XI.69, S. Frommer and R. Worley, 4F; ibid., 31.I-10.II.70, S. Frommer, R. Worley and L. La Pré, 3M, 1F; ibid., 4-11.II.73, A. Tabet, 7F; ibid., 12.IV.75, J.B. Tucker, 1M; ibid., J.B. Turner, 1F. *Nevada:* Austin, 12.VIII.40, D.E. Hardy, 1M. *New Mexico:* Grant Co., Gila Nat. For., Cherry Creek Cpgd., 21 km. n. Silver City, 2250m, 3-4.VIII.80, J.E. and W.M. O'Hara, 23M, 9F; Socorro Co., Magdalena Mts., 19.VIII.51, E.L. Kessel, 2F.

MEXICO: *Chihuahua:* Mesa del Huracan, 108°15'N 30°04'W, 7400', 21-25.VII.64, J.E.H. Martin, 2M. *Durango:* Rio Chico, 20 mi. w. Durango, 7000', 10.VIII.64, J.F. McAlpine, 1M; 10 mi. w. El Salto, 9000', 21.VI.64, J.F. McAlpine, 1M; 6500', VIII.64, J.F. McAlpine, 1M; 24 mi. w. La Ciudad, 7000', 28.VI.64, W.R.M. Mason, 2M. *Mexico:* El Pedregal, 5-8.VII.78, G. and M. Wood, 16M, 2F. *Sinaloa:* El Palmito, 6400', 2.VII.64, J.F. McAlpine, 1M. (Deposited in AMNH, CAS, CNC, DMW, JEOH, MSU, UASM, UCR, UKL and USNM.)

3.9 The S. geniculata group

North American species of the *S. geniculata* group have a short aristomere 3 (0.35-0.45 head height), proboscis of average length and at least one of the following two characteristics: one pair of median marginal setae on T_{1+2} (Fig. 8), and/or a long surstylus which extends beyond apex of cerci by more than preapical width of surstylus (Figs. 70-71).

3.9.1 Siphona geniculata (De Geer)

Musca geniculata De Geer, 1776: 38.

Crocuta geniculata: Coquillett, 1910: 518.

Siphona geniculata: Mesnil, 1965: 866 (redescription).-- Following New World records are based on misidentifications. Coquillett, 1897: 76.-- Aldrich, 1905: 444.-- Aldrich, 1934: 109.-- Sabrosky and Arnaud, 1965: 1064.-- Cortés and Hichins, 1969: 57.-- Cortés and Campos, 1970: 98.-- Arnaud, 1978: 458.

Siphona analis Meigen, 1824: 157.-- Herting, 1972: 3.

Siphona cinerea Meigen, 1824: 156.-- Herting, 1972: 4.

Bucentes cinereus Latreille, 1809: 339.

Siphona meigenii St. Fargeau and Serville, 1828: 501.

Stomoxys minuta Fabricius, 1805: 282.

Siphona nigrovittata Meigen, 1824: 157.-- Herting, 1972: 11.
Siphona tachinaria Meigen, 1826: 156.-- Herting, 1972: 13.
Musca urbanis Harris, 1780: 153.

The type of *Musca geniculata* De Geer is lost (Herting, per. comm.). Nevertheless the species now established as *S. geniculata* (whether or not the original one) is readily recognized so a neotype is not required.

Recognition.-- Specimens are relatively large for *Siphona*. Eye height and proboscis length average, flagellomere 1 and aristomere 3 short. Most specimens with above average number of hairs (10-20) on upper parafacial and frontal plate. This is one of two species with both a long surstylus and 1 pair of strong median marginal setae on T_{1+2}. Abdominal vitta present, broader than average, and obscured by dense pruinosity. Postsutural dorsocentral setae four.

With median marginal setae on T_{1+2} and a long surstylus, *S. geniculata* is unlike any species other than *S. hokkaidensis*. Generally, shape and length of male flagellomere 1 permits separation of specimens of these species, since most *S. hokkaidensis* specimens with median marginals on T_{1+2} have large first flagellomeres (as in Fig. 32).

Description.-- Specimens examined: 6 males, 3 females from North America, 16 males and 11 females from Europe.

Length: 4.5-6.5mm.

Male. *Head* (Fig. 28). *Colouration:* frontal vitta testaceous, brown to reddish-brown; gena and lower parafacial white to light yellow; fronto-orbital plate and upper parafacial yellow to dark brown, darkest on orbital plate; scape and pedicel testaceous to fuscous; flagellomere 1 fuscous to black; palpus yellow, apex slightly infuscate in most specimens; proboscis reddish-brown or fuscous. *Eye:* size average for genus, 0.786-0.833 head height (Fig. 13), broad, widest at center, evenly rounded along anterior margin. *Macrotrichia:* cluster of 10-20 hairs on upper parafacial and frontal plate in most specimens; vibrissal angle average in most specimens, more heavily setose than average in a few specimens with 2 or 3 setae and several setulae in addition to vibrissa and several hairs. *Antenna:* flagellomere 1 short, 0.420-0.484 head height (Fig. 14), rounded distally along ventral margin; aristomere 3 short for genus, in most specimens 0.35-0.45 head height. *Mouthparts:* proboscis length average for genus, 2.02-2.50 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or gray finely mixed with brown, not vittate; tegula testaceous to reddish-brown; wing yellowish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, 25 specimens examined, all with four [males and females]. *Acropod:* claws and pulvilli average to slightly larger than average.

Preabdomen. Colouration: dark, faintly vittate; T_4, T_5 and broad vitta on T_{1+2} and T_3 black in ground colour, rest of preabdomen yellow in ground colour; surface dark gray or brownish-gray on areas of black ground colour, dark brown to black around macrotrichial insertions; areas of yellow ground colour with surface light brown or tawny. *Macrotrichia:* 1 pair median marginals on T_{1+2}; 1 or 2 pair strong lateral marginals on T_{1+2} and T_3.

Genitalia (Fig. 91). Four examined, including 3 from European specimens. Apex of surstylus extended beyond apex of cerci by more than preapical width of surstylus. *Aedeagus:* slope of distiphallus even with angle of basiphallus (not bent); antero-ventral margin dentate; in profile parallel-sided and elongate; apex truncate or nearly so.

Female. As described for male except as follows.

Head (Fig. 50). Palpus equal or slightly longer than in males.

Preabdomen. Colouration: dark, not vittate; black in ground colour, surface gray finely mixed with light brown.

Geographical distribution (Fig. 91).-- A wide ranging species in the Palearctic Region; introduced and established in the lower Fraser Valley of British Columbia. It has not, to date, been recorded elsewhere in North America. It is unlikely *S. geniculata* will spread beyond its restricted range unless its introduced host, *Tipula paludosa*, extends its range, or *S. geniculata* adapts to a native *Tipula* species.

Chorological affinities.-- At present *S. geniculata* occupies a narrow range in North America, and it is uncertain whether this species interacts with other *Siphona* species in the area (especially *S. hokkaidensis*).

Phylogenetic relationships (Fig. 105).-- The sister species to this species is probably a Paleactic species. In North America, *S. hokkaidensis* is its most closely related species.

3.9.2 Siphona hokkaidensis Mesnil

Siphona hokkaidensis Mesnil, 1957: 36.-- Mesnil, 1965: 869.-- Herting, 1967: 9 (comparison of *S. hokkaidensis* Mesnil and *S. silvarum* Herting).

Siphona silvarum Herting, 1967: 9. **New synonymy.**

Type material examined.-- *Siphona hokkaidensis* Mesnil, HOLOTYPE, female, labelled: "Obihiro [Hokkaido, Japan]/ S. Takano [handwritten label]"; "295 [green label]"; "Siphona/ hokkaidensis Mesnil/ L.P. Mesnil det., 1970"; "Type [red label]"; "EX/ L.-P. MESNIL/ COLLECTION 1970" (CNC).

Siphona silvarum Herting, HOLOTYPE, male, labelled [exact line data not recorded]: "ex larvae *Tipula irrorata* Mg. [handwritten label]"; "Mooswald. Freiburg [West Germany]

L.B. IV.1958 [handwritten label]"; "Siphona silvarum Hert. L.P. Mesnil det., 1970"; "TYPE [red label]"; "EX L.-P. MESNIL COLLECTION 1970" (CNC). Two puparia accompany type on same pin.

Recognition.-- Eye height, flagellomere 1 and proboscis lengths varied. Aristomere 3 short and thick in most specimens. Most eastern specimens without marginal setae on T_{1+2} and with flagellomere 1 subtriangular (Fig. 31). Specimens from Alberta, Saskatchewan and Manitoba with short slender flagellomere 1 (Fig. 30). Northwestern specimens varied, a few with 1 or a pair of median marginal setae on T_{1+2} and very large flagellomere 1 (Fig. 32). A few specimens with above average number of setae on vibrissal angle, up to 4 present. Apex of surstylus extended far beyond apex of cerci, distiphallus truncate or nearly so. Most specimens with four postsutural dorsocentral setae.

Specimens with median marginal setae on T_{1+2} are similar to *S. geniculata*, and are discussed under "Recognition" of that species.

Eastern specimens of *S. hokkaidensis* form a homogeneous group, readily distinguished in most instances by the subtriangular (male), apically truncate (both sexes) flagellomere 1 and short (and in most males, thick) aristomere 3. *S. hokkaidensis* specimens from other regions varied, as discussed above. In all regions male genitalia permit separation of this species from others, because of the very long surstylus and characteristic distiphallus (Fig. 71).

Description.-- Specimens examined: 271 males, 144 females. *Length:* 3.5-5.5mm.

Male. *Head* (Figs. 30-32). *Colouration:* frontal vitta testaceous, brown to reddish-brown; gena and parafacial light yellow to light brown; fronto-orbital plate brown to dark brown; scape, pedicel, and in a few specimens a portion of flagellomere 1 above aristal insertion yellow, testaceous, or (in a few specimens) fuscous; flagellomere 1 reddish-brown, fuscous to black; palpus yellow, in a few specimens apex infuscate; proboscis testaceous to fuscous. *Eye:* size very varied, 0.711-0.820 head height (Fig. 13), slender and narrowed below center to broad and evenly rounded along anterior margin. *Macrotrichia:* vibrissal angle with 2-4 setae and several hairs, in addition to vibrissa. *Antenna:* length and shape of flagellomere 1 extremely varied, 0.426-0.667 head height (Fig. 14), treated below under geographic variation; aristomere 3 short for genus, in most specimens 0.35-0.45 head height and thickened almost to tip. *Mouthparts:* length of proboscis very varied, 1.96-2.53 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or gray finely mixed with brown in most specimens, 3 brown vittae visible in a few specimens; tegula testaceous to fuscous; wing yellowish hyaline; legs average. *Macrotrichia:*

postsutural dorsocentrals, 7 specimens with three, 91 with four. *Acropod:* claws and pulvilli average-sized.

Preabdomen. Colouration: extremely varied, vittate in all but a very few specimens; eastern specimens, black ground colour on T_5, vittate or entirely black on T_4, vittate on T_{1+2} and T_3, rest of preabdomen yellow in ground colour; areas black in ground colour with surface blue-gray, dark brown to black around macrotrichial insertions; areas yellow in ground colour with yellow or light brown surface; specimens from Alberta, Saskatchewan and Manitoba with ground colour as for eastern specimens, surface predominantly light coloured, brownish-gray on areas of black ground colour, yellow or light brown on areas of yellow ground colour; vitta visible though faint through light coloured pruinosity; dark areas around macrotrichial insertions very reduced; pattern in western specimens very varied, most specimens similar to eastern specimens, a few similar to specimens from Alberta, Saskatchewan and Manitoba, and a few specimens unique - more extensively black in ground colour, yellow ground colour restricted to extreme lateral edge of T_{1+2} and antero-lateral edge of T_3, not vittate; surface predominantly blue-gray, wide area around macrotrichial insertions dark brown to black. *Macrotrichia:* median marginals on T_{1+2} present or absent, data recorded in Fig. 81; 1 or 2 pair strong lateral marginals on T_{1+2} and T_3, data recorded for T_3 in Fig. 81.

Genitalia (Fig. 71). Twenty-seven examined, including 1 from a European specimen. Apex of surstylus extended beyond apex of cerci by more than preapical width of surstylus. *Aedeagus:* slope of distiphallus even with that of basiphallus, or distiphallus very slightly bent downward; antero-ventral margin dentate; in profile nearly parallel-sided; apex truncate or nearly so.

Female. As described for male except as follows.

Head (Fig. 51). Length of palpus subequal or slightly longer than in males.

Preabdomen. Colouration: in all geographic regions ground colour pattern very similar, not vittate, yellow ground colour restricted to extreme lateral edge of T_{1+2} and antero-lateral edge of T_3; eastern specimens very dark, surface blue-gray to gray, wide areas around macrotrichial insertions dark brown to black, black ground colour very evident through light coloured pruinosity; specimens from Alberta, Saskatchewan and Manitoba with surface brownish-gray, dark areas around macrotrichial insertions reduced, ground colour obscured by light coloured pruinosity; specimens from Washington, British Colombia, Northwest Territories, Yukon and Alaska with surface very varied, from light gray or brownish-gray with light appearance as in Alberta, Saskatchewan and Manitoba specimens, to very dark like most eastern specimens.

Variation, with notes about synonymy.-- Polymorphism in *S. hokkaidensis* was investigated in some detail to provide the basis for a taxonomic decision regarding morphs. Two character systems in particular were amenable to analysis. These were shape of flagellomere 1 and number and position of abdominal setae. These characteristics were at least in part geographically distributed, as shown in Fig. 81.

Three basic shapes of the flagellomere 1 were recognized in males of *S.hokkaidensis*, permitting specimens to be sorted into three groups on that basis. The three antennal types, designated 1, 2 and 3, are illustrated in Figs. 30-32. Intermediate forms were few and limited to specimens from western North America in regions where more than one antennal type were present. Specimens with intermediate first flagellomeres were assigned the antennal type they most closely resembled.

Females of *S. hokkaidensis* have smaller first flagellomeres than males, so the three antennal types recognized in males could not be applied to females. Females were treated in a fourth catagory ("f" in Fig. 81).

Except for one sample from northern Quebec (Indian House Lake), all male specimens examined from Ontario eastward had a type 2 antenna. In other characteristics this group varied little.

Males from Alberta, Saskatchewan and Manitoba also formed a homogeneous group, sharing type 1 antenna, a slightly larger eye and shorter proboscis than average for the species, and similar colouration. This group was called *S. hokkaidensis* "a" and treated separately from other specimens of the species (*S. hokkaidensis* "b") in the Hubbs-Hubbs diagrams. Locality records for specimens of this group are represented by squares on the distribution map (Fig. 81).

Throughout most of the Northwest Territories type 3 antenna predominated among specimens examined. In Alaska and the Yukon all three antennal types were represented in localities in relatively close proximity to one another, with mixed series recorded in two samples.

Abdominal setae reflected a similar geographic pattern to the one exhibited by antennal variation (Fig. 81). Median marginal setae on T_{1+2} were present in a greater percentage of specimens with type 3 antenna than any other. However, in northwestern North America specimens with antennal types 1 and 2 had a higher occurrence of median marginals than they did anywhere else. The number of lateral marginals on T_3 also conformed to this pattern (Fig. 81).

My interpretation of these data is as follows. Whatever events produced polymorphism in *S. hokkaidensis*, they apparently have not resulted in permanent interruption of gene flow between morphs, as exemplified by the heterogeneous populations in northwestern North America. Therefore I regard all morphs as members of a single species, *S. hokkaidensis*.

Most distinctive of all were specimens with type 1 antenna from Alberta, Saskatchewan and Manitoba, for which reason they were treated separately in the Hubbs-Hubbs diagrams. Unfortunately, there were too few specimens of *S. hokkaidensis* from the western provinces to permit detailed interpretation of the relationship between *S. hokkaidensis* "a" and "b". Primarily because specimens with a type 1 antenna were found in northwestern North America with other characters varied, I concluded that *S. hokkaidensis* "a" does not represent a new species or subspecies. Furthermore, two autapomorphies support the present interpretation of *S. hokkaidensis* as one species: male genitalia are unique and almost unvaried over the North American range of the species, and the arista is thickened in most specimens irrespective of antennal type.

Differences between specimens with antennal types 2 and 3 are slight, so there is little reason to suspect they represent more than morphs of a single species. Dr. Herting noted (per. comm.) that both antennal types are represented in European specimens of "*S. silvarum*", so the situation is geographically widespread.

As a result of study of abdominal setae, *Siphona silvarum* Herting was synonymized with *Siphona hokkaidensis* Mesnil. Mesnil first described *S. hokkaidensis* from a female specimen from Hokkaido, Japan (1957), then redescribed the species from European specimens in his treatment of *Siphona* in Lindner's "Die Fleigen der palaearktischen Region"

(1965). Herting (1967) compared European and Japanese specimens and noted the former lacked median marginals on T_{1+2} and differed in colouration from the latter. At the time neither form was known from North America, and their distributions appeared disjunct in the Palearctic Region. There was sufficient reason for believing the forms represented two species, so Herting (1967) named *S. hokkaidensis* of Mesnil, 1965 (not 1957) *Siphona silvarum*.

From data presented herein the varied nature of abdominal setae in *S. hokkaidensis* is documented. The type of *S. silvarum* conforms in all respects to the present interpretation of *S. hokkaidensis* - bearing a type 2 antenna and lacking median marginals on T_{1+2} - so it has been synonymized with *S. hokkaidensis*.

Geographical distribution (Fig. 81).-- Holarctic, in Palearctic Region ranging over Europe, USSR and Japan; in Nearctic Region widely distributed in Canada, Alaska and extreme northeastern United States. This species has a more northern distribution in Canada than any other *Siphona* species.

Chorological affinities.-- This species is sympatric with another *S. geniculata* group member, *S. medialis*, along the southern edge of its range. It is widely sympatric with *S. maculata*, *S. intrudens*, *S. lutea*, *S. multifaria* and *S. cristata*.

Phylogenetic relationships (Fig. 105).-- In North America, this species is most closely related to *S. geniculata*. However, several European species resemble *S. hokkaidensis*, and one of these is probably its sister species.

3.9.3 Siphona medialis new species

Holotype.-- Male, labelled: "Cranberry I. [Island]/ Lockeport, N.S. [Nova Scotia, Canada]/ 25.VII.1958/ J.R. Vockeroth" (CNC).

Allotype.-- Female, same data as holotype (CNC).

Derivation of specific epithet.-- *S. medialis* is the only wide ranging North America species that is characterized by strong median marginal setae on T_{1+2}. *S. medialis* is named in recognition of this attribute.

Recognition.-- A dark coloured species with a very large eye, short flagellomere 1 and average-sized proboscis. Aristomere 3 short in most specimens. Legs of western specimens very dark, specimens from other areas with legs average to darker than average. Preabdomen black in ground colour (not vittate), with 1 pair median marginal setae on T_{1+2}. Postsutural dorsocentral setae three or four.

This is one of the more distinctive species, with its dark colouration, large eye, median marginals on T_{1+2} and (in most specimens) dark legs. It can only be confused with the two other species with median marginals on T_{1+2}.

Male specimens of *S. hokkaidensis* have a smaller eye, longer surstylus and are lighter coloured than *S. medialis*. In addition, most specimens of *S. hokkaidensis* with median marginals on T_{1+2} are from northwestern North America and have large first flagellomeres (as in Fig. 32).

S. medialis is most easily distinguished from *S. geniculata* by colouration, relative position of apices of surstylus and cerci, and in almost all instances by range differences.

Description.-- *Length:* 4.0-5.5mm.

Male. *Head* (Fig. 29). *Colouration:* frontal vitta testaceous to reddish-brown; gena and parafacial white to light brown; fronto-orbital plate light to dark brown, darkest on orbital plate; scape and pedicel black in most specimens, fuscous in a few; flagellomere 1 black; palpus yellow, in a few specimens apex infuscate; proboscis fuscous to black. *Eye:* very large for genus, 0.786-0.833 head height (Fig. 13), broad, widest at center, evenly rounded along anterior margin. *Macrotrichia:* vibrissal angle average in most specimens, a few specimens more heavily setose than average with 2-4 setae in addition to vibrissa and several hairs. *Antenna:* flagellomere 1 on average slightly longer than, but similar in shape to, that of *S. geniculata*, 0.439-0.533 head height (Fig. 14); aristomere 3 short for genus, in most specimens 0.35-0.45 head height. *Mouthparts:*

proboscis length average for genus, 2.00-2.51 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or gray finely mixed with brown in most specimens, 3 brown vittae visible in a few specimens; tegula reddish-brown to black; wing yellowish to cinereous hyaline; leg colouration geographically varied; specimens examined from Washington, Idaho, Oregon and California with femora and tibiae fuscous in most specimens, reddish-brown in a few; specimens from other areas average to darker than average, reddish-brown or fuscous portion covering dorsal and posterior surfaces of fore femur in a few specimens, reddish-brown portions on mid and hind femora not covering more than apical two-thirds, most extensive dorsally, tibiae predominantly yellow. *Macrotrichia:* postsutural dorsocentrals, 11 specimens with three, 14 with four. *Acropod:* claws and pulvilli average-sized.

Preabdomen. Colouration: dark; most specimens not vittate, black in ground colour, surface blue-gray, gray or brownish-gray, dark brown to black around macrotrichial insertions; in a very few specimens T_{1+2} and T_3 laterally yellow in ground colour, surface light brown. *Macrotrichia:* one pair median marginals on T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 72). Seven examined. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent slightly or sharply downward from angle of basiphallus; antero-ventral margin dentate; apex broad in profile.

Female. As described for male except as follows.

Head (Fig. 52). Palpus equal or slightly longer than in males.

Preabdomen. Colouration: not vittate; as described for average male.

Geographical distribution (Fig. 94).-- Transcontinental; widely distributed in western United States, restricted to region along Canada-United States border in central and eastern North America.

Habitat.-- I have collected specimens of this species once, in southwestern Utah. Adults were swept from a damp meadow of sedge and grass. Specimens collected by J.F. McAlpine and R.L. Hurley in Ninette, Manitoba, were caught in *Poa*-sedge meadows (label data).

Chorological affinities.-- This species is sympatric with *S. hokkaidensis* along the northern edge of its range. In addition to being transcontinental, *S. medialis* is widely distributed in western United States, and is sympatric with all *Siphona* species of America north of Mexico except *S. pisinnia*, *S. illinoiensis* and *S. floridensis*.

Phylogenetic relationships (Fig. 105).-- This species is related to the *S. geniculata - S. hokkaidensis* lineage of the *S. geniculata* group.

Paratypes.-- Twenty-six males, 40 females. CANADA: *Alberta:* 15mi. e. Morley, 23.VI.62, W.R.M. Mason, 1M; 13mi. n. Banff, Banff-Jasper Hwy., 4500', 26.VII.55, R. Coyles, 1F. *Manitoba:* Ninette, 14.VI.58, J.F. McAlpine, 1M; ibid., R.L. Hurley, 1F; 2mi. e. Douglas, 27.VII.58, N.B. Chillcott, 1F. *New Brunswick:* Kouchibouguac N.P., 7,13.VII.77, J.F. McAlpine, 2M, 1F; Birch Cove, nr. Chamcook, 4.VII.65, G.E. Shewell, 4M. *Nova Scotia:* Cranberry I., Lockeport, 18,20,24-25, 27-28,30.VII.58, J.R. Vockeroth, 2M, 6F; Halifax Co., Lawrencetown, 19-20.VII.67, D.M. Wood, 2M, 1F. *Prince Edward Island:* Green Gables, Cavendish Beach, 22.VII.67, D.M. Wood, 2F. *Quebec:* mi. 139, rte. 58, La Verendrye Prov. Pk., 29.VI, 1.VII.65, D.M. Wood, 2M, 3F.

USA: *California:* Nevada Co., Sagehen, 5mi. nw. Hobart Mills, 20.VI.54, M.T. James, 2F; ibid., 25.VI.54, R.M. Bohart, 1F; ibid., 2.VII.54, E.I.Schlinger, 1F; ibid., 22.VI.72, R.A. Belmont, 1F; ibid., 15.VII.64, M.E. Irwin, 1M, 1F; Merced Co., Dos Palos, 7.V.49, 1F; Sierra Co., 4.8mi. se. Sierraville, 14.VI.59, G.W. Byers, 1M. *Colorado:* Estes Pk., 7500', 2.VII.61, C.H. Mann, 2M, 1F; Hartsel, 20.VI.40, A.L. Melander, 2M, 2F; Tenn. Pass, 26.VII.17, J.M. Aldrich, 1F; 2061, 1F. *Idaho:* Moscow, 30.V.11, J.M. Aldrich, 1M. *Maine:* Sagahadoc Co., Popham Beach, 15.VII.71, P. Ward, 1F. *Michigan:* Iosco Co., 30.VII.48, R.R. Dreisbach, 1F. *Minnesota:* Eaglesnest, 30.VI.59, W.V. Balduf, 1F. *Montana:*

Bozeman, 20.VI.06, 1M; Powell Co., Nigger Hill, VII, W.M. Mann, 1F. *Oregon:* Klamath Co., Mare's Egg Spring, 12.VI.64, J. Schuh, 2M; ibid., Fort Klamath, 26.VI.52, E.I. Schlinger, 1F. *Utah:* Grizzly Ridge Camp, 30mi. n. Vernal, 8400', 8.VII.61, J.G. Chillcott, 1F; Kane Co., Dixie Nat. For., Duck Ck. Cpgd., 50km. se. Cedar City, rte. 14, 2620m, 16-17.VIII.80, J.E. and W.M. O'Hara, 1M, 5F. ***Washington:*** Pullman, 23.V.18, 4.VI.22, A.L. Melander, 1M, 1F. (Deposited in CNC, INHS, JEOH, MSUB, UASM, UCD, UCR, UKL, USNM and WSUP.)

3.10 The S. futilis group

Members have an average length proboscis, large eye and narrow, short to average length flagellomere 1. *S. brunnea* is a provisional member.

3.10.1 Siphona futilis van der Wulp

Siphona futilis van der Wulp, 1890: 125.-- Aldrich, 1905: 444.-- Guimarães, 1971: 170.

Bucentes futilis: Curran, 1932: 13 (in key).

Bucentes ceres Curran, 1932: 14. **New synonymy.**

Siphona ceres: Guimarães, 1971: 170.-- Arnaud, 1978: 458.

Notes about synonymy.-- Curran included *S. futilis* in his 1932 key to adults of North American *Siphona* species.

However, Curran's key appears to have been written primarily from published species descriptions. There is no indication that Curran examined specimens of *S. futilis* prior to his description of *S. ceres*. I regard the type of *S. ceres* as conspecific with the lectotype of *S. futilis*.

Type material examined.-- *Siphona futilis*, 14 syntypes from BMNH, 1 syntype from USNM. These specimens comprise two species, both described subsequent to *futilis*: *Siphona ceres* (Curran) and *Siphonopsis plusiae* (Coquillett). I have chosen to retain as valid nominal species *plusiae* because it is type-species of *Siphonopsis*, and its life history has been investigated under that specific epithet (Bloeser, 1914). Therefore the lectotype here designated for *Siphona futilis* is conspecific with *ceres*, and replaces that name.

LECTOTYPE, male, labelled: "Co-/ type [round yellow-ringed label]"; "Omilteme,/ Guerrero, [Mexico]/ 8000 ft./ July. H.H. Smith."; "B.C.A. Dipt. II./ Siphona/ futilis,/ v.d.W."; "♂"; "Central America./ Pres. by/ F.D. Godman./ O. Salvin./ 1903-172" (BMNH). My lectotype label "LECTOTYPE/ Siphona/ futilis/ van der Wulp/ O'Hara designation/ Selected 1981 [red bordered label]" has been attached to this specimen.

PARALECTOTYPES, 7 specimens of *Siphonopsis plusiae* (Coq.) (6 BMNH, 1 USNM). Seven specimens (BMNH) conspecific with lectotype: MEXICO, GUERRERO: same data as lectotype, 2M, 2F; Xucumanatlan, 7000ft, VII, H.H. Smith, 2M. VERACRUZ:

Orizaba, XII.1887, H.H.S. & F.D.G., 1F. [BMNH specimens damaged in transit, most in very poor condition.] To these specimens both paralectotype and determination labels have been attached. One specimen in the USNM was not examined.

Bucentes ceres, HOLOTYPE, female, labelled: "Antigua, Guat[emala]./ 5-V-1931/ D.M. Bates 506"; "Bucentes/ TYPE/ ceres ♀/ Curran/ No. [red label]"; "Bucentes/ ceres/ Curran [handwritten det. label]" (AMNH). My determination label "Siphona/ futilis/ van der Wulp/ det./ J.E. O'Hara 1981" has been attached to this specimen.

Recognition.-- Eye large, flagellomere 1 short and proboscis length average. Scape and pedicel fuscous to black. Palpus yellow in most specimens, slightly infuscate apically in a few specimens. Male preabdomen light coloured, vittate. Female preabdomen darker than in male; without vitta. Distiphallus bent sharply downward from angle of basiphallus, narrow in profile, apex sloped sharply postero-ventrally in most specimens. Postsutural dorsocentral setae three in most specimens (95%).

Eye and proboscis sizes are very similar between *S. futilis* and *S. illinoiensis*. *S. futilis* has a shorter flagellomere 1. There are also slight colour differences: scape and pedicel are dark coloured in *S. futilis* and light coloured in *S. illinoiensis*; female preabdomen broadly vittate in *S. illinoiensis*, entirely dark in ground colour in *S. futilis*. There is a marked similarity between distiphalli of these species, attesting to their close relationship. The main difference is the distiphallus is bent sharply downward from angle of basiphallus in *S. futilis* and is even with basiphallus in *S. illinoiensis*.

Since *S. futilis* and *S. illinoiensis* are allopatric, the only species likely to be confused with the former is *S. brunnea*. Head characteristics are similar, but dark colouration of *S. brunnea* in combination with other features readily separate these species (see *S. brunnea*, "Recognition").

Description.-- Specimens examined: 66 males, 53 females. *Length:* 4.0-5.0mm.

Male. *Head* (Fig. 34). *Colouration:* frontal vitta testaceous to reddish-brown; gena and parafacial white, light yellow to light brown; fronto-orbital plate light to dark brown, darkest on orbital plate; scape and pedicel fuscous to black; flagellomere 1 black; palpus yellow, slightly infuscate at apex in a few specimens; proboscis reddish-brown or fuscous. *Eye:* large for genus, 0.847-0.911 head height (Fig. 13), broad, widest at center, evenly rounded along anterior margin. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 0.450-0.517 head height (Fig. 14), slender, rounded distally along ventral margin; length of aristomere 3 average for genus. *Mouthparts:* proboscis length average for genus, 2.10-2.41 head height (Fig. 15).

Thorax. *Colouration:* dorsum average, blue-gray or gray finely mixed with brown in most specimens, 3 brown vittae visible in a few specimens; tegula testaceous to reddish-brown; wing yellowish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, 39 specimens with three, 2 with four. *Acropod:* claws and pulvilli average-sized.

Preabdomen. *Colouration:* light coloured, vittate; yellow ground colour laterally on T_{1+2}, T_3 and antero-laterally on T_4, rest black in ground colour; vitta long and narrow; areas black in ground colour with surface blue-gray, gray or brownish-gray, dark brown to black around macrotrichial insertions; areas yellow in ground colour with surface yellow to light brown; pattern varied in a few specimens, slightly greater or lesser than average amounts of black ground colour. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 73). Seven examined. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent sharply downward from angle of basiphallus; antero-ventral margin dentate; in profile narrow, apex sloped sharply postero-ventrally in most specimens.

Female. As described for male except as follows.

Head (Fig. 53). Palpus longer than in males in a few specimens.

Preabdomen. Colouration: darker than male, without vitta; most specimens black in ground colour, a very few laterally yellow in ground colour on T_{1+2}; surface as described for male.

Geographical distribution (Fig. 96).-- Recorded from central Mexico to Costa Rica.

Chorological affinities.-- The range of this species encompasses most of the range of *S. tropica*, and the entire known ranges of *S. brunnea*, *S. rizaba*, *S. akidnomyia* and *S. longissima*. The ranges of *S. futilis* and *S. pisinnia* overlap in central Mexico. *S. futilis* is allopatric to sister species *S. illinoiensis*.

Phylogenetic relationships (Fig. 107).-- This species is sister species to *S. illinoiensis*, from which it differs only slightly.

3.10.2 *Siphona illinoiensis* Townsend

Siphona illinoiensis Townsend, 1891: 368.-- Coquillett, 1897: 76 (as syn. of *S. geniculata*).-- Aldrich, 1905: 444 (as syn. of *S. geniculata*).-- Bezzi and Stein, 1907: 382 (as syn. of *S. geniculata*).-- Sabrosky and Arnaud, 1965: 1064.

Type material examined.-- One syntype, herein designated LECTOTYPE, male [nec female], labelled: "9"; "Robertson/ S. Illinois"; "Siphona/ illinoiensis/ Tws"; "Type"; "COTYPE/ Siphona/ illinoiensis/ Tns. [red label]" (UKL). My lectotype label "LECTOTYPE/ Siphona/ illinoiensis Tnsd./ O'Hara designation/ Selected 1981 [red bordered label]" has been attached to this specimen.

Townsend described *S. illinoiensis* from 2 specimens. The KSU collection has only one specimen labelled "COTYPE"; the one herein designated lectotype. However, the KSU collection has a male specimen of *S. illinoiensis* with same locality label as the type. It is probably the missing syntype.

Recognition.-- Eye large, flagellomere 1 and proboscis lengths average. Scape and pedicel yellow to testaceous. Male preabdomen light coloured, vittate. Female preabdomen slightly darker than male, with short broad vitta. Slope of distiphallus even with that of basiphallus. Distiphallus narrow in profile, apex sloped sharply postero-ventrally in most specimens. Postsutural dorsocentral setae three in most specimens (86%).

Similarities and differences between *S. illinoiensis* and *S. futilis* are discussed under "Recognition" of the latter species.

Within central and eastern North America, specimens of *S. cristata* and *S. multifaria* may be mistaken for *S.*

illinoiensis. Most male specimens of *S. illinoiensis* can be distinguished by characteristics given in key and by comparing specimen measurements with those presented in the Hubbs-Hubbs diagrams. Male genitalia of *S. illinoiensis* are relatively unvaried, and sufficiently different from *S. cristata* and *S. multifaria* to aid in identifications.

Not all female specimens of *S. illinoiensis* can be distinguished from those of *S. cristata* and *S. multifaria*. Eye and proboscis sizes can yield ambiguous results. In most specimens the light brownish-gray, non-vittate female preabdomen of *S. illinoiensis* can be distinguished from the abdominal colouration of *S. cristata* and *S. multifaria*. However, decisions regarding subtle colour differences are untrustworthy if specimens of only one species are at hand.

Description.-- Specimens examined: 217 males, 163 females. *Length:* 3.0-5.0mm.

Male. *Head* (Fig. 1). *Colouration:* frontal vitta yellow, testaceous to reddish-brown; gena and parafacial white to light yellow; fronto-orbital plate light yellow to light brown or brown, darkest on orbital plate; scape, pedicel, and in a few specimens a portion of flagellomere 1 above aristal insertion yellow to testaceous; flagellomere 1 fuscous; palpus yellow; proboscis testaceous to reddish-brown. *Eye:* large for genus, 0.807-0.909 head height (Fig. 13), broad, widest at center, evenly rounded along anterior margin. *Macrotrichia:* average for genus. *Antenna:*

flagellomere 1 0.500-0.596 head height (Fig. 14), slender, rounded distally along ventral margin; length of aristomere 3 average for genus. *Mouthparts:* proboscis length average for genus, 1.93-2.49 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or gray finely mixed with brown in most specimens, 3 brown vittae visible in a few specimens; tegula testaceous; wing yellowish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, 91 specimens with three, 15 with four. *Acropod:* claws and pulvilli average-sized (Fig. 4).

Preabdomen. Colouration: light coloured, vittate; most specimens black in ground colour on T_4, T_5 and medially on T_{1+2} and T_3, rest of preabdomen yellow in ground colour; areas black in ground colour with surface brownish-gray, brown to black around macrotrichial insertions; areas yellow in ground colour with surface light yellow or light brown to tawny; pattern varied in a few specimens, areas black in ground colour slightly more, or less, extensive. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 9). Twenty examined. As described for *S. futilis*, except slope of distiphallus even with that of basiphallus in most specimens, slightly bent downward in a few.

Female. As described for male except as follows.

Head (Fig. 54). Palpus longer and thicker than in males in most specimens.

Preabdomen. Colouration: average specimens slightly darker than male, with yellow ground colour restricted to lateral edge of T_{1+2} and antero-lateral edge of T_3, dark vitta short and broad; surface colour and variation as decribed for male.

Geographical distribution (Fig. 92).-- Widely distributed in eastern United States.

Chorological affinities.-- This uniquely distributed species is parapatric or narrowly sympatric with *S. hokkaidensis*, *S. maculata*, *S. lutea*, *S. medialis* and *S. cristata* along the northern edge of its range. Widely sympatric with *S. illinoiensis* are *S. intrudens* and *S. multifaria*. *S. illinoiensis* is allopatric to sister species *S. futilis*.

Phylogenetic relationships (Fig. 107).-- This species is sister species to the Mexican species *S. futilis*.

3.10.3 *Siphona brunnea* new species

Holotype.-- Male, labelled: "MEX. [Mexico] Chis. [Chiapas] 9600ft./ Zontehuitz, nr. S. Crist. [San Cristobal de las Casas]/ 17 May 1969/ W.R.M. Mason" (CNC).

Allotype.-- Female, same data as holotype (CNC).

Derivation of specific epithet.-- *Brunneus* is Latin for brown. This species is named for its very dark brown colouration.

Recognition.-- Eye large, flagellomere 1 short and proboscis length average. A dark brown species, with apical half of palpus fuscous or black, wing brownish hyaline and legs in some specimens darker than average. Male tarsal claws slightly longer than average. Male preabdomen not vittate, surface dark brown with a light coloured band across anterior portion of each tergite. Female abdominal colouration varied. Surstylus slightly longer than cerci. Distiphallus bent sharply downward from basiphallus, narrow and truncate in profile. Postsutural dorsocentral setae four.

An easily recognized species, quite different from members of the Mexican *S. tropica* group. Similar in head characteristics to *S. futilis*, but distinguishable on basis of colouration, number of postsutural dorsocentrals and in particular by structure of distiphallus.

Description.-- *Length:* 4.5-5.0mm.

Male. *Head* (Fig. 35). *Colouration:* frontal vitta dark brown to reddish-brown; gena and parafacial light brown; fronto-orbital plate dark brown; antenna black; palpus yellow basally, apical half fuscous or black; proboscis fuscous or black. *Eye:* large for genus, 0.833-0.843 head height (Fig. 13), broad, widest above center, slightly narrowed below center. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 0.463-0.510 head height (Fig. 14), short and distally rounded; length of aristomere 3 average for genus. *Mouthparts:* proboscis length average for genus, 2.35-2.44 head height (Fig. 15).

Thorax. Colouration: dorsum dark brown; tegula black; wing brownish hyaline; legs average to darker than average, reddish-brown regions covering dorsal and posterior surfaces of fore femur and distal half of mid and hind femora in two specimens. *Macrotrichia:* postsutural dorsocentrals, four in all specimens. *Acropod:* claws and pulvilli slightly larger than average.

Preabdomen. Colouration: dark, not vittate; black in ground colour except for extreme lateral edge of T_{1+2} and T_3; surface dark brown with light bands across anterior 0.25 of T_3, T_4 and T_5. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 74). One examined. Apex of surstylus extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent sharply downward from angle of basiphallus; antero-ventral margin dentate; in profile narrow, apex truncate.

Female. As described for male except as follows.

Head (Fig. 55). Length of palpus subequal in males and females.

Preabdomen. Colouration: light bands slightly wider than in male; one female with same ground colour pattern as male, other female vittate, with yellow ground colour dorso-laterally on T_{1+2}.

Geographical distribution (Fig. 97).-- Known only from Chiapas, Mexico.

Chorological affinities.-- From label data this species has evidently been collected from the same locality as *S. akidnomyia*, though at a different time of year.

Phylogenetic relationships (Fig. 107).-- Due to the highly derived nature of this species, it is difficult to place with certainty. It is here interpreted as a member of the *S. futilis* group on the basis of its large eye and general habitus.

Paratypes.-- One male, 1 female. MEXICO: *Chiapas:* Zontehuitz, nr. San Cristobal de las Casas, 9600', 17.V.69, W.R.M. Mason, 1M, 1F. (Deposited in CNC.)

3.11 The S. tropica group

Group characteristics are: long to very long proboscis and a very long flagellomere 1, the latter in profile apically wide and broadly rounded along ventral margin. Most species have a large eye.

3.11.1 Siphona tropica (Townsend)

Phantasiosiphona tropica Townsend, 1915: 93.-- Townsend, 1936: 150 (in key to genera of the Siphonini), Townsend, 1940: 286 (redescription of genus).-- Guimarães, 1971: 169.

Bucentes tropica: Curran, 1932: 13 (in key).

Type material examined.-- PARATYPE, male [nec female], labelled: "Granada/ Nicaragua/ Coll. Baker"; "V/ 77 [tiny handwritten label]"; "Paratype No./ 19954/ U.S.N.M. [red label]"; "Phantasiosiphona/ tropica/ Tns. det/ Sabrosky" (USNM).

Recognition.-- Eye large, flagellomere 1 and proboscis long. Wing brownish hyaline, with single setula on bend of R_1 in most specimens (89%). Preabdomen light coloured, vittate in both sexes. Distiphallus distinctive, slope even with that of basiphallus, apex narrow and pointed in profile. Postsutural dorsocentral setae three.

Similar to *S. longissima* and *S. rizaba* in proboscis length, and to latter in eye height. Most specimens of *S. tropica* are readily identified by presence of a setula distally on R_1. No other Middle American species is known to exhibit this character state. Structure of the male distiphallus is particularly diagnostic for this species.

Description.-- Specimens examined: 14 males, 6 females. *Length:* 4.0-5.0mm.

Male. *Head* (Fig. 38). *Colouration:* frontal vitta testaceous to dark brown; gena and parafacial white, light yellow to light brown; fronto-orbital plate light to dark brown, darkest on orbital plate; antenna fuscous; palpus yellow; proboscis testaceous, reddish-brown to fuscous. *Eye:* large for genus, 0.860-0.891 head height (Fig. 13), slender, widest above center, narrowed below center. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 very long and broad for genus, 0.654-0.745 head height (Fig. 14), rounded distally along ventral margin and in most specimens produced slightly forward distally along dorsal margin; length of aristomere 3 average for genus. *Mouthparts:* proboscis long for genus, 2.76-3.02 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or gray finely mixed with brown in most specimens, 3 brown vittae visible in a few specimens; tegula fuscous to black; wing brownish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, three in all 19 specimens examined; wing, 19 specimens examined: one seta on both wings in 14 specimens; 1 seta on one wing only in 3 specimens; setae absent, 2 specimens. *Acropod:* claws and pulvilli average-sized.

Preabdomen. Colouration: vittate; varied, yellow ground colour ranging from laterally on T_{1+2} and antero-laterally on T_3 to laterally on T_{1+2}, T_3 and antero-laterally on T_4, surface yellow, light brown to tawny; areas black in ground colour with surface blue-gray, gray to brown, darker around macrotrichial insertions. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 78). Four examined. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* slope of distiphallus even with that of basiphallus (not bent); antero-ventral margin dentate; apex narrow and pointed in profile.

Female. As described for male except as follows.

Head (Fig. 57). Length of palpus subequal in males and females.

Preabdomen. Colouration: vittate; yellow ground colour laterally on T_{1+2} and antero-laterally on T_3, otherwise as described for male.

Geographical distribution (Fig. 101).-- Recorded from southern Mexico to western Colombia.

Habitat.-- Recorded from cloud forest at 5100' in Puebla, 5 mi. ne. of Teziutlán. In Veracruz (Fortín de las Flores) specimens of this species were collected between 2500-3000' (from label data).

Chorological affinities.-- Though widely distributed throughout Central America and southeastern Mexico, records do not show specimens of this species as having been collected with those of other Middle American *Siphona* species.

Phylogenetic relationships (Fig. 106).-- Relationships among *S. tropica* group members are unclear, for reliable synapotypies have not been discovered. *S. tropica* and *S. rizaba* are tentatively grouped as sister species on the basis of a very large eye and the loss of hooks on the distiphallus.

3.11.2 Siphona rizaba new species

Holotype.-- Male, labelled: "Orizaba, Ver[acruz].,/ Mex[ico]. 8/12-22/61/ R&K Dreisbach" (MSU). Terminalia in microvial on pin below specimen.

Allotype.-- Female, same data as holotype, with Reinhard determination label: Bucentes/ tropica/ Tns. R. [Reinhard initial]" (MSU).

Derivation of specific epithet.-- This species is named after the type-locality, Orizaba, from which the first letter has been removed.

Recognition.-- Eye large, flagellomere 1 and proboscis long. Wing yellowish to brownish hyaline. Preabdomen light coloured, vittate in both sexes. Externally without good diagnostic characteristics. Apex of surstylus extended slightly to far beyond apex of cerci. Distiphallus slightly bent downward from basiphallus, apex rounded in profile. Postsutural dorsocentral setae three.

This species is the least distinctive of the *S. tropica* group. It shares the general characteristics of the other members of the group, but lacks good diagnostic features. *S. tropica* specimens without a single setula on R_1 can be confused with this species. Dissection of male genitalia is advisable where ratios flagellomere 1: eye and head heights are near upper values for *S. rizaba* and lower values of *S. tropica* and *S. longissima* (Figs. 14,16).

Description.-- *Length:* 4.0-5.0mm.

Male. *Head* (Fig. 38). *Colouration:* frontal vitta testaceous to brown; gena and lower parafacial white, light yellow to light brown; upper parafacial and frontal plate light brown to dark brown; orbital plate brown to dark brown; scape and pedicel testaceous to reddish-brown or fuscous; flagellomere 1 fuscous; palpus yellow; proboscis testaceous to reddish-brown. *Eye:* large for genus, 0.846-0.870 head height (Fig. 13), slender, widest at center, slightly narrowed below center. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 long and broad, 0.593-0.648 head height (Fig. 14), broadly rounded distally along ventral margin; length of aristomere 3 average for genus. *Mouthparts:* proboscis long for genus, 2.74-3.03 head height (Fig. 15).

Thorax. *Colouration:* dorsum average, blue-gray or gray finely mixed with brown in most specimens, 3 brown vittae visible in a few specimens; tegula reddish-brown to fuscous; wing yellowish to brownish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, three in all specimens. *Acropod:* claws and pulvilli average-sized.

Preabdomen. *Colouration:* vittate; T_4, T_5 and vitta on T_{1+2} and T_3 black in ground colour, surface gray, brownish-gray or brown, darker around macrotrichial insertions; T_{1+2} and T_3 laterally yellow in ground colour, surface yellow to light brown. *Macrotichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 79). Four examined. Apex of surstylus extended slightly beyond to more than preapical width of surstylus beyond apex of cerci. *Aedeagus:* distiphallus bent slightly downward from angle of basiphallus; antero-ventral margin dentate; apex rounded in profile.

Female. As described for male except as follows.

Head (Fig. 58). Palpus subequal in length in males and females..

Preabdomen. *Colouration:* short vittate; yellow ground colour restricted to T_{1+2}, otherwise as described for male.

Geographical distribution (Fig. 98).-- Recorded from two localities in Veracruz, Mexico.

Chorological affinities.-- This species is evidently sympatric with *S. futilis* and *S. tropica*, but specimens of it have not been caught together with those of any other species.

Phylogenetic relationships (fig. 106).-- See this heading under *S. tropica*.

Paratypes.-- Three males, 2 females. MEXICO: *Veracruz:* Orizaba, 12-22.VIII.61, R. and K. Dreisbach, 1M, 2F; Cordoba, 13,20.VII.66, J.S. Buckett, M.R. and R.C. Gardner, 2M; (Deposited in MSU and UCD.)

3.11.3 Siphona longissima new species

Holotype.-- Male, labelled: "MEX. [Mexico] Chis. [Chiapas] 10mi NE./ San Cristobal [de las Casas]/ 13.V.69 7500'/ H.J. Teskey" (CNC). Terminalia in microvial on pin below specimen.

Derivation of specific epithet.-- From *longissimus*, Latin for "longest". *S. longissima* has the longest proboscis of species described in this paper.

Recognition.-- Eye large and flagellomere 1 long. Proboscis very long, one specimen with longest proboscis of any recorded North American species (3.2X head height). Wing brownish hyaline. Tarsal claws intermediate in size between average and large. Preabdomen vittate in male. Distiphallus distinctive, bent sharply downward from basiphallus, antero-ventral margin with small hooks, apex narrow and pointed in profile. Postsutural dorsocentral setae three. Female of species unknown.

Most similar to *S. tropica* and *S. rizaba*. Other than characteristic sizes of eye, flagellomere 1 and proboscis, *S. longissima* can be distinguished by shape of distiphallus and the small hooks (as in *S. macronyx* and *S. akidnomyia*) along its antero-ventral margin.

Description.-- *Length:* 4.5-5.0mm.

Male. *Head* (Fig. 37). *Colouration:* frontal vitta brown; gena and parafacial light brown; fronto-orbital plate brown to dark brown, darkest on orbital plate; antenna fuscous to black; palpus yellow; proboscis fuscous. *Eye:* slightly larger than average for genus, 0.796-0.850 head height (Fig. 13), slender, widest above center, narrowed below center. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 very long and broad for genus, 0.650-0.667 head height (Fig. 14), rounded distally along ventral margin; length of aristomere 3 average for genus. *Mouthparts:* proboscis long for genus, 2.74-3.20 head height (Fig. 15).

Thorax. Colouration: dorsum darker than average, dark brown; tegula fuscous to black; wing brownish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, three in all specimens. *Acropod:* claws and pulvilli intermediate in size between average and large.

Preabdomen. Colouration: vittate; yellow ground colour laterally on T_{1+2} and T_3, surface yellow; areas black in ground colour with surface gray to brown, darker around macrotrichial insertions. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 77). Two examined. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus sharply bent downward from angle of basiphallus; antero-ventral margin with small hooks (similar to *S. macronyx* and *S. akidnomyia*); apex narrow and pointed in profile.

Female. Unknown.

Geographical distribution (Fig. 100).-- Recorded from southern Mexico.

Chorological affinities.-- Specimens of this species have been caught in the same area as those of *S. futilis* and *S. akidnomyia*, but not on the same days (from label data).

Phylogenetic relationships (Fig. 106).-- The position of this species within the *S. tropica* group is tentatively as sister species to the highly derived *S. akidnomyia*.

Paratypes.-- Two males. MEXICO: *Chiapas:* 3mi. n. San Cristobal de las Casas, 7000', 29.V.69, H.J. Teskey, 1M. *Distrito Federal:* Desierto de Los Leones, X.65, N.L.H. Krauss, 1M. (Deposited in CNC and USNM.)

3.11.4 Siphona akidnomyia new species

Holotype.-- Male, labelled: "MEX. [Mexico] Chis. [Chiapas] 9600ft./ Zontehuitz, nr. S. Crist. [San Cristobal de las Casas]/ 25 June 1969/ W.R.M. Mason" (CNC). Terminalia in microvial on pin below specimen.

Allotype.-- Female, labelled: "MEXICO, Chiapas/ Mt. Tzontehuitz/ 9400' 12mi. NE San/ Cristobal [de las Casas] 27.V./ 1969 B.V. Peterson" (CNC).

Derivation of specific epithet.-- Derived from the Greek for feeble (*akidnos*) fly (*myia*). This is in reference to *Siphona* in general, which lack the size and strength of their larger relatives.

Recognition.-- Eye size average, flagellomere 1 and proboscis long. Palpus long, apex infuscate in most specimens. Wing brownish hyaline. Male tarsal claws large. Male preabdomen dark, broadly vittate, female preabdomen average vittate. Distiphallus unique, short and broad in profile with small hooks on antero-ventral margin. Postsutural dorsocentral setae three.

Closest in appearance to, yet readily distinguished from, *S. tropica*, *S. rizaba* and *S. longissima*. *S. akidnomyia* is the darkest of these species (though lighter than *S. brunnea*), and has a shorter proboscis, smaller eye and longer tarsal claws than the others. The infuscate palpus is very large for *Siphona*, especially in the female. The distiphallus has small hooks along its antero-ventral margin (as in *S. macronyx* and *S. longissima*), and a very distinctive shape.

Description.-- *Length:* 4.0-5.0mm.

Male. *Head* (Fig. 36). *Colouration:* frontal vitta brown; gena and parafacial white to light brown; fronto-orbital plate brown to dark brown, darkest on orbital plate; antenna fuscous to black; palpus yellow, apex infuscate; proboscis fuscous. *Eye:* size average for genus, 0.781-0.804 head height (Fig. 13), slender, widest at center, slightly narrowed below center. *Macrotrichia:* average for genus. *Antenna:* flagellomere 1 long and broad for genus, 0.585-0.660 head height (Fig. 14), broadly rounded distally along ventral margin; length of aristomere 3 average for genus. *Mouthparts:* palpus longer than average for genus; proboscis long for genus, 2.49-2.66 head height (Fig. 15).

Thorax. Colouration: dorsum average to dark brown; tegula fuscous; wing brownish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, three in all specimens. *Acropod:* claws and pulvilli large.

Preabdomen. Colouration: broadly vittate; laterally on T_{1+2} and laterally or antero-laterally on T_3 yellow in ground colour, surface yellow; areas black in ground colour with surface blue-gray, gray to brown, darker around macrotrichial insertions. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals on T_{1+2} strong.

Genitalia (Fig. 76). Five examined. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus slightly or sharply bent downward from angle of basiphallus; narrow section between basiphallus and distiphallus longer than average; antero-ventral margin with small hooks (similar to *S. macronyx* and *S. longissima*); in profile distiphallus short and broad, apex pointed.

Female. As described for male except as follows.

Head (Fig. 59). Palpus larger than in males, very long for genus, apex infuscate in one female.

Preabdomen. Colouration: vitta average; surface colour as described for male, except slightly lighter.

Geographical distribution (Fig. 99).-- Recorded from southern Mexico.

Chorological affinities.-- Evidently sympatric with *S. longissima*, *S. brunnea* and *S. futilis*, specimens of this species have been recorded from the same localities as the former two species, but were not collected on the same dates.

Phylogenetic relationships (Fig. 106).-- This is the most highly derived species of the *S. tropica* group. Intragroup relationships are difficult to interpret without additional characters. *S. longissima* is tentatively placed as sister species to *S. akidnomyia* on the basis of larger than average tarsal claws.

Paratypes.-- Four males, 1 female. MEXICO: *Chiapas:* Mt. Tzontehuitz, 9400', 12mi. e. San Cristobal de las Casas, 27.V.69, B.V. Peterson, 1M; 8mi. ne. San Cristobal de las Casas, 7500', 15.V.69, H.J. Teskey, 1M; San Cristobal de las Casas, 7087', 13,28.VI.69, B.V. Peterson, 1M,1F. *Distrito Federal:* Desierto Leones, III,IV,V.65, N.L.H. Krauss, 1M. (Deposited in CNC and USNM.)

3.12 The S. macronyx group

This group contains one highly autapotypic species, *S. macronyx*. The characteristics of this species (see "Recognition" below) are such that it cannot, at this time, be placed in one of the other North American *Siphona* species groups. Further study and additional characters might indicate that *S. macronyx* is a derived member of one of the other recognized groups. If so, then it should be placed in that group.

3.12.1 Siphona macronyx new species

Holotype.-- Male, labelled: "Pullman, Wash. [Washington, USA]/ Malaise Trap."; "R.W. Dawson/ May 6 1969" (WSUP). Terminalia in microvial on pin below specimen.

Allotype.-- Female, same data as holotype except date May 13, 1969 (WSUP).

Derivation of specific epithet.-- From the Greek words for large claw, *makros* and *onyx*, after this attribute of the species.

Recognition.-- Head and characteristic habitus due to broad eye, above average number of setae and setulae on vibrissal angle, short flagellomere 1 and dark colouration. Proboscis average length. Male tarsal claws large. Preabdomen dark, in male broadly vittate, in female entirely black in ground colour. Distiphallus bent sharply downward from angle of basiphallus with several small hooks along antero-ventral margin. Postsutural dorsocentral setae three.

The derived features of this species are such that specimens are not closely similar to those of any other species.

Description.-- *Length:* 4.0-5.5mm.

Male. *Head* (Fig. 33). *Colouration:* frontal vitta orange, testaceous to reddish-brown; gena and parafacial light brown in most specimens, light yellow in a few; fronto-orbital plate brown to dark brown; scape, pedicel, and in a few specimens a portion of flagellomere 1 above aristal insertion yellow, testaceous to reddish-brown; flagellomere 1 fuscous to black; palpus yellow; proboscis reddish-brown to fuscous. *Eye:* size average for genus, 0.742-0.804 head height (Fig. 13), broad, widest at center, evenly rounded along anterior margin. *Macrotrichia:* vibrissal angle with cluster of 3-6 setae and several setulae in addition to vibrissa. *Antenna:* flagellomere 1 short, 0.403-0.500 head height (Fig. 14), rounded distally along ventral margin; length of aristomere 3 average for genus. *Mouthparts:* proboscis length average for genus, 2.00-2.34 head height (Fig. 15).

Thorax. Colouration: dorsum average, blue-gray or gray finely mixed with brown in most specimens, 3 brown vittae visible in a few specimens; tegula testaceous to reddish-brown; wing brownish hyaline; legs average. *Macrotrichia:* postsutural dorsocentrals, 60 specimens with three, 1 with four [males and females]. *Acropod:* claws and pulvilli large.

Preabdomen. Colouration: dark, broadly vittate; T_4, T_5 and vitta on T_{1+2} and T_3 black in ground colour, surface gray to brown, black around macrotrichial insertions; yellow ground colour laterally on T_{1+2} and T_3 in most specimens, surface yellow to light brown; in 2 specimens yellow ground colour very reduced. *Macrotrichia:* median marginals absent from T_{1+2}; lateral marginals strong.

Genitalia (Fig. 75). Two examined. Apex of surstylus even with or extended slightly beyond apex of cerci. *Aedeagus:* distiphallus bent sharply downward from angle of basiphallus; antero-ventral margin with small hooks (similar to *S. longissima* and *S. akidnomyia*); apex broad in profile.

Female. As described for male except as follows.

Head (Fig. 56). In most specimens gena yellow, parafacial and frontal plate bright yellow tinged with brown (near golden); length of palpus slightly longer than in male in a few specimens.

Preabdomen. Colouration: not vittate; black in ground colour except for faint traces of yellow ground colour laterally on T_{1+2} in a few specimens; surface light blue-gray, gray or brownish-gray, mixed with brown medially.

Geographical distribution (Fig. 88).-- Known only from Washington and western Idaho.

Chorological affinities.-- The small known range of this species is sympatric with the northern limits of the ranges of western species *S. lurida*, *S. oligomyia* and *S. pacifica*. *S. macronyx* is parapatric or sympatric with *S. hokkaidensis*, *S. maculata*, *S. intrudens*, *S. lutea*, *S. multifaria*, *S. medialis* and *S. cristata*, though specimens of it have not been collected with specimens of any of these species (from label data).

Phylogenetic relationships (Fig. 103).-- See discussion under species group heading above.

Paratypes.-- Eleven males, 49 females. USA: *Idaho:* Moscow Mt., 5.VII.19, A.L. Melander, 1M. *Washington:* Whitman Co., Almota, 27.IV.72, W.J. Turner, 1M, 2F; Jefferson Co., falls outside Olympic Nat. Pk. entrance, 15km. ne. Quinault, P.H. Arnaud, Jr., 1F; Asotin Co., Fields' Spr. St. Pk., 15.VI.72, W.J. Turner, 3F; Dewatto, 7.VI.06, J.M. Aldrich, 1F; Chelan Co., Squillchuck St. Pk., 9mi. se. Wenatchee, 17,VI.73, M. Jackson, 1F; Lyle Grove, Pullman, 3.VI.69, H.S. Telford, 1F; ibid., 10.VI.11, A.L. Melander, 1F; Pullman, WSU Campus-bee area, 3.V.71, W.J. Turner, 1M; Pullman, nr. SCS Pond, WSU, 29.V.71, W.J. Turner, 1F; Pullman, 9,11-12,14,19,28,30.V, 1,4,6.VI.65, R.D. Akre, 4M, 9F; ibid., 7,18.V.66, 5-6,8,15-17,22,25-29.V, 1.VI.69, R.W. Dawson, 4M, 29F. (Deposited in CAS, USNM and WSUP.)

4. PHYLOGENETIC INTERPRETATION

4.1 Introduction

In the ensuing pages phylogenetic aspects of *Siphona* species are considered. The approach I have taken is cladistic, wherein character states are evaluated and polarized according to their inferred plesiotypic (ancestral) or apotypic (derived) nature. Assuming only apotypic states to be analyzable in phylogenetic interpretation, these states are arranged in a nested pattern of hierarchies to produce a cladogram (a diagram depicting a succession of apotypic character states representing hypothetical phylogenetic relationships) most parsimonious with the data available.

Since publication of Hennig's English version of his book "Phylogenetic Systematics" (1966a), numerous practical accounts of cladism have been published (eg. Griffiths, 1972; Ross, 1974; Eldredge, 1979). The reader is referred to these sources for a detailed exposition of the cladistic method of phylogenetic analysis used here.

The term monophyly is subject to different interpretations. As used here it excludes paraphyly, being monophyly in Hennig's sense (equivalent to holophyly of Ashlock, 1971). Within the Siphonini a monophyletic group of genera is distinguished on the basis of two shared derived character states:

1) anal vein extended to wing margin at least as fold (groundplan for the Tachinidae is anal vein terminating in wing membrane), and

2) three katepisternal setae, of which postero-dorsal is strongest and antero-ventral is longer than antero-dorsal (groundplan for at least the Siphonini is antero-dorsal seta longer than antero-ventral).

Within the context of a tribal revision it would be appropriate to consider formal recognition of this group in the classification. The present study does not warrant such action, especially with limits of the Siphonini subject to various interpretations. So that I may identify this group of siphonines herein I refer to it informally as the *Siphona* group. Genera included are: *Aphantorhapha* Townsend, *Asiphona* Mesnil, *Ceranthia* Robineau-Desvoidy, *Peribaea* Robineau-Desvoidy, *Pseudosiphona* Townsend, *Siphona* Meigen and *Siphonopsis* Townsend.

With the exception of *Siphona* and *Peribaea*, the genera form an assemblage of species of unclear relationship. Of these genera I have examined many undescribed species from Middle and South America and suspect other inadequately collected areas also harbour new species. Recognized genera do not bear well such scrutiny, and I predict a generic revision will reduce their number. Due to their similarities I refer to them collectively as *Ceranthia s. lat.* to distinguish them from *Siphona* and *Peribaea* and to focus attention on their unsettled status.

Siphona is probably monophyletic, as shown by proboscis structure. The proboscis is long and geniculate, with the labella at least as long as prementum and at least (in most species considerably more than) eye height in length (Fig. 1,18-59).

Most species of *Ceranthia s. lat.* have a labellar disc similar to that of a housefly. In North American species in which it is elongate (*Siphonopsis* and *Pseudosiphona* species in particular), it can be distinguished by characteristics given in the "Reclassification" section.

Similarity between the proboscis of several Oriental and eastern Palearctic *Actia* species and *Siphona* is also discussed in the "Reclassification" section.

A detailed comparison of male genitalia of *Siphona* species with those of species of *Ceranthia s. lat.* will probably corroborate the monophyletic origin of *Siphona* species. Currently, states of the major characters of male genitalia within taxa of the *Siphona* group have not been polarized, so a cladistic analysis cannot be conducted. However, preliminary studies suggest most genitalic features are plesiotypic in *Siphona*, even though the combination of features that contribute to the general habitus of the male genitalia in that genus is unique. A detailed study of the male genitalia of *Ceranthia s. lat.* taxa (including many undescribed species) is needed to determine the synapotypic features of this character complex in *Siphona* species. Such a study might also provide the necessary framework upon which to build a classification for taxa of *Ceranthia s. lat.*

4.2 Character analysis

4.2.1 General notes

I have recognized 15 characters as suitable for phylogenetic analysis of North American *Siphona* species. Each is discussed below in relation to delimitation and polarization of states. Difficulties peculiar to delimitation of mensural characters are discussed under Character 1, eye height.

Out-group and in-group comparisons have been conducted to polarize character states. The out-group is *Ceranthia s. lat.* (defined in the previous section). The in-group is world *Siphona* species, as represented by specimens made available to me during the course of this study (see world list for described species examined).

A character weighting system has not been used, as explained in the "Reconstructed phylogeny" section.

One character useful for identifications has been excluded from the analysis. This character, number of postsutural dorsocentral setae, is either 3 or 4, and in many species the number is of diagnostic value. Both states are widely distributed in the out-group and in-group, without concordance among other character states.

Consequently the apotypic state could not be determined; if it had been, then the number of reversals necessary to account for its present distribution would probably have negated its usefulness.

In the following section and in the character matrix (Fig. 102) an a represents the inferred plesiotypic state. The first apotypic state is given an **A**. Other apotypic states not assignable to a transformation series with the first are denoted by successive capitals letters; **B**, **C**, **D**, etc. The order in which these are named refers only to their position in the matrix, starting from top. Transformation series are denoted by superscripts, negative numbers being used only with mensural characters in which the plesiotypic state is inferred to be an average value (ie. eye height).

4.2.2 Characters and states

Character 1. **Male eye height**

This character and proboscis length are difficult to analyse because of their complex pattern of inter- and intraspecific distribution. As such they represent transformation series of phylogenetic importance, albeit without the relatively unambiguous delimitation of states common to meristic characters. I have employed a practical solution to this problem: delimitation of states based on apparent groupings about mean values (refer to Figs. 13,15), with consideration of concordance with other characters for species of ambiguous placement.

The theoretical danger here is introduction of circularity into the analysis by allowing perceived relationships among certain characters to affect delimitation of others. To counter this departure from standard phylogenetic practice, I discuss doubtful species placements under each species group. Despite these drawbacks I regard the characters eye height and proboscis length as important to the elucidation of *Siphona* phylogenetics, and their treatment in the manner indicated necessary for their interpretation.

The ranges given below for each eye height state are based only on consideration of species under revision, in accordance with criteria discussed above. The plesiotypic state is inferred to be an average-sized eye, as this state is the most widespread throughout the genus and across species groups. Both small and large eyes are considered apotypic.

a - average-sized, mean between 0.76-0.82 head height.
A^{-2} - very small eye of *S. lurida*.
A^{-1} - small, though larger than eye of *S. lurida*, and less than 0.76 head height.
A^{1} - larger than average, between 0.82-0.85 head height.
A^{2} - very large, greater than 0.85 head height.

Character 2. Male flagellomere 1

Six independent states are recognized in size and shape of male flagellomere 1. The states of this character are too varied in taxa of *Ceranthia s. lat.* to permit their polarization by out-group comparisons. Since no state is distributed among examined species of world *Siphona* in a manner suggestive of plesiotypy, all states are presumed apotypic. Relationships between states are unknown (other than divisions of A, B and C), so they cannot be treated as a transformation series.

A^1 - narrow, average length to long, broadly rounded apically along ventral margin such that dorsal edge is apically pointed.

A^2 - shaped as in A^1 though shorter.

B^1 - relatively broad in profile, average length to long, dorsal and ventral surfaces parallel, rounded or slightly truncate apically along ventral margin, not pointed as in A.

B^2 - shaped as in B^1 but very long.

C^1 - narrow, short, rounded along ventral margin, not pointed.

C^2 - shaped as in C^1 but of average length.

D - triangular, apically truncate. Here *S. hokkaidensis* is treated separately according to the shape of flagellomere 1 of eastern North American specimens (Fig. 31), though other morphs resemble closely states C and F.

E - short and apically rounded.

F - very long, wide apically in profile and broadly rounded along ventral margin.

Character 3. Proboscis length

The plesiotypic state for *Siphona* at one time must have been a short proboscis, perhaps of the sort exhibited by *Siphonopsis* species. To my knowledge no extant *Siphona* species has a proboscis shorter than *S. floridensis* or *S. maculata*, so the truly ancestral state of the genus is no longer represented.

I have treated proboscis length as a transformation series from very short (plesiotypic) to very long (apotypic), as polarized by out-group comparisons. A regression from a derived to less derived state (ie. a reduction in proboscis length) is inferred to only have occurred in *S. lutea* and *S. akidnomyia*.

An alternative exists to this polarization scheme. The *S. maculata* group is monophyletic, based on shape of flagellomere 1, and contains two character states interpreted as symplesiotypies: a short proboscis and weak lateral marginal setae on T_{1+2}. Since both states are virtually limited to that group, either of two explanations account for their restricted distribution: (1) the *S. maculata* group branched from the main lineage of *Siphona* early in the history of the genus, and retained to the present ancestral states which became modified in the main lineage, or (2) the *S. maculata* group is relatively young, and states limited to it are apotypic. Due to lack of corroborative evidence for the second hypothesis I consider the first more parsimonious with available data.

Criteria for delimitation of character states is discussed under eye height.

a - very short, less than 1.55X head height.
A' - short, mean between 1.55-1.8X head height.
A^2 - slightly shorter than average, 1.8-2.1X head height.
A^3 - average-sized, 2.1-2.5X head height.
A^4 - long, 2.5-2.7X head height.
A^5 - very long, greater than 2.7X head height.

Character 4. **Aristomere 3**

This character is represented by a transformation series which is easily polarized by in-group comparisons. Species with the derived states are apparently monophyletic in *Siphona*, for the states are in accord with other data. However, a few species in the ex-group (eg. *Ceranthia flavipes* and *C. abdominalis*) also possess state **A'**.

a - average length for *Siphona*, 0.50-0.65 head height.
A' - shorter than average, 0.35-0.45 head height.
A^2 - short as in **A'** and thickened to near tip.

Character 5. **Vibrissal angle**

States were determined by in-group and out-group comparisons. Although the states seem to represent a transformation series, no other evidence suggests the bearers of **A**^{1} and **A**^{2} (*S. macronyx* and *S. lurida* respectively) are closely related.

a - average condition, 2-3 setae and several hairs in addition to vibrissa.

A^1 - 3-6 setae and several setulae and hairs in addition to vibrissa.

A^2 - heavily setose, up to 10 setae and several setulae and hairs in addition to vibrissa.

Character 6. **Male colouration**

Colouration within the out-group is too varied to be useful in polarization of states in *Siphona*.

The most prevalent male colour pattern among *Siphona* species, and that least in accordance with other characters, is predominantly blue-gray over most of thorax (where it is mixed with light brown) and abdomen, the latter medially vittate and laterally yellow in ground colour on T_{1+2} and T_3. This state is regarded as plesiotypic, as are slight deviations from it.

a - given above.

A - abdomen black in ground colour, not vittate, deep blue-gray as basic pattern.

B^1 - thorax dark in ground colour at least dorsally, abdomen partially to entirely yellow.

B^2 - body yellow in ground and surface colour.

C - abdomen black in ground colour, not vittate, surface predominantly brownish-gray.

D^1 - brown pruinosity over most of dorsal surfaces.

D^2 - as in D^1 only darker brown.

Character 7. **Wing setulae on R_1**

With varied frequency, R_1 wing setulae are present among species of a number of siphonine genera. Except in a few instances their presence is evidently autapotypic. This is as true of the genus *Siphona* as any other. There appears to be a predisposition for expression of wing setulae on R_1 among these genera, so species sharing this trait are not necessarily closely related.

Among siphonines setulae on R_1 is expressed in one of three ways: vein setulose along its length; or limited to a row along the bend; or represented by one or two setulae near the bend. Most non-*Siphona* species with R_1 setulose belong to the first two categories. *Siphona bevisi* Curran and *S. setinerva* Mesnil (both African) are in the first category, other examined *Siphona* species belong to the third category - *S. lutea, S. oligomyia, S. tropica* and *S. grandistylum* Pandellé (the last from the Pyrenees).

a - setulae absent.

A - one or two setulae near bend of R^1.

Character 8. **Wing setulae on R_{4+5}**

Wing setulae on R_{4+5} between bifurcation of R_{2+3} and R_{4+5} and crossvein r-m is characteristic of the Siphonini, and represents the plesiotypic state in *Siphona*. As with R_1 however, the apotypic state in *Siphona* has been independently derived in other genera and presumably within *Siphona* as well. Of the species under revision only *S. lutea* has R_{4+5} setulose beyond r-m. Other *Siphona* species with this condition (of species examined) are *S. bevisi* Curran, *S. setinerva* (Mesnil) and *S. unispina* (Mesnil) (all from Africa). The African species resemble one another and further analysis may indicate they belong in the same group. They do not share characteristics other than wing setulae with *S. lutea*, so are probably not closely related to it.

a - vein R_{4+5} setulose between bifurcation of R_{2+3} and R_{4+5} and crossvein r-m.

A - vein R_{4+5} setulose beyond r-m.

Character 9. Male tarsal claws

The groundplan for *Siphona* is small tarsal claws. Large tarsal claws of males are present in a very few species of other *Siphona* group genera (eg. state A' in *Asiphona brunnescens* (Vill.)). These observations suggest the apotypic states, especially A', are easily acquired and seldom indicative of a monophyletic origin.

a - average-sized, length of claw subequal to width of tarsomere 5 (Figs. 4,6).

A^1 - intermediate in size between a and A^2.

A^2 - large claw, length subequal to length of tarsomere 5 (Fig. 5).

Character 10. **Median marginal setae on R_{4+5}**

I am unaware of any *Siphona* group species not belonging to *Siphona* that possess a pair of median marginals on T_{1+2}. Nevertheless, consideration of more distantly related tachinids reveals that median marginals on T_{1+2} are widespread, indicating their absence from most members of the *Siphona* group almost certainly results from suppression of this attribute. This may explain why very few specimens of *S. cristata* and *S. multifaria* have median marginals on T_{1+2}, and why a few specimens of other species have slight development of a median marginal hair on T_{1+2} such that it is distinctly stronger than others to either side.

a - absent.

A^1 - a significant proportion of specimens with median marginals on T_{1+2} (here interpreted as a regression from A^2).

A^2 - virtually all specimens with one pair median marginal setae on T_{1+2}.

Character 11. **Lateral marginal setae on T_{1+2}**

Most species of the *Siphona* group other than those belonging to *Siphona* have weak lateral marginal setae on

T_{1+2}, although more distantly related tachinids in most species have strong setae in this position. As with median marginals on T_{1+2}, lateral marginals probably result from suppression.

In *Siphona* weak lateral marginals on T_{1+2} are almost exclusive to species of the *S. maculata* group. Since this state is widespread in the out-group, it is interpreted as symplesiotypic in the *S. maculata* group (also see discussion under character 3).

a - setae absent or one pair weakly developed.
A - one pair strong setae.
B - two pair strong lateral marginal setae on T_{1+2} in significant number of specimens.

Character 12. **Male sternum 5**

Of male specimens examined, only two unrelated *Siphona* species, *S. oligomyia* and *S. cuthbertsoni* Curran, possess a sternum 5 in which the antero-lateral arms are hooked inward. This condition is characteristic of *Siphonopsis* species, which form either the sister group to *Siphona* or branch from the *Ceranthia* lineage. Be that as it may, there is no other indication the hooked state of sternum 5 is plesiotypic in *Siphona*. In fact, the most parsimonious explanation is independent evolution of the hooked state among *Siphona* species rather than its loss in all but a very few.

a - antero-lateral margins smoothly rounded (Fig. 10).
A - antero-lateral margins hooked inward (Fig. 11).

Character 13. **Antero-ventral margin of distiphallus**

By far the most prevalent condition of the distiphallus by out-group and in-group comparisons is a dentate antero-ventral margin. This is presumed plesiotypic. The difference between the dentate state and one in which small hooks are present (**A^1**) is slight, hence is more likely to occur in unrelated taxa than are states **A^2** and **A^3**.

a - dentate.
A^1 - small hooks (Figs. 75-77).
A^2 - hooks medium in size (Fig. 60).
A^3 - large hooks, margin U-shaped in anterior view (Fig. 62).

Character 14. **Shape of distiphallus**

The plesiotypic shape of the distiphallus in *Siphona* is unknown. I have chosen to regard all shapes without apparent apotypic features as plesiotypic. This conservative approach should ensure that species with the same apotypic shape have a high probability of sharing a uniquely derived state.

A transformation series could not be discerned from distiphallus shapes exhibited, so each apotypic state is treated independently.

a - without recognizable apotypic shape (ie. not necessarily plesiotypic, but treated as such).

A - subtriangular, apex sharply pointed in profile (Figs. 60,62).

B - anterior margin of distiphallus slightly indented in profile about one third of its length from apex (Figs. 66-68).

C - anterior and posterior surfaces of distiphallus nearly parallel in profile, apex truncate (Figs. 70-71).

D - narrow in profile, sloped postero-ventrally (Figs. 9,73).

E - narrow in profile, apically truncate (Fig. 74).

F - broad and short in profile (Fig. 76).

G - narrow in profile, subtriangular, apex pointed (Figs. 77-78,80).

Character 15. **Surstylus length**

The most prevalent condition of the surstylus and one least in agreement with other character states is presumed plesiotypic.

a - apex of surstylus even with or extended slightly beyond apex of cerci.

A - apex of surstylus extended beyond apex of cerci by more than preapical width of surstylus.

4.3 Reconstructed phylogeny

4.3.1 Introduction

In reconstructing the phylogenies presented in Figs. 103-107, I have not employed a character weighting system. I recognize its advantages when applied to certain types of data, as lucidly demonstrated by Hecht and Edwards (1976, 1977) for example, but such a system is not appropriate to all situations. With respect to *Siphona*, the characters analyzed are inadequate to permit elucidation of relationships among most species groups, so where character weighting would have been most useful it cannot be applied. Furthermore, with relatively few characters of broad import, the most parsimonious reconstructed phylogeny for each species group has few alternatives. I have depicted only one phylogenetic scheme for each species group, but I discuss problem species placements below, and consider the strengths and weaknesses of the character states involved. Under these circumstances I consider the utility of a character weighting system negated.

Figs. 103-107 illustrate inferred relationships among North American *Siphona* species. Exclusion of Palearctic species from these diagrams is not indicative of more distant relationships between regions, for indeed the *Siphona* faunas of the Nearctic and Palearctic Regions are intimately associated. My analysis of Palearctic *Siphona* species has not been sufficiently detailed to warrant species placements beyond group. In general, *Siphona* species from other regions have been considered to an even lesser extent.

The approach I have taken is thus:

1) inferred relationships among North American species are discussed under each species group;

2) alternative phylogenies are considered;

3) the 11 described Palearctic *Siphona* species (excluding Holarctic species and *S. seyrigi* Mesnil of the Canary Islands) are used to test my hypotheses concerning delimitation of species groups; and

4) *Siphona* species from the Neotropical and Afrotropical Regions are considered where their character states are relevant to the discussion.

4.3.2 The S. maculata group

The ancestor to extant members of the *S. maculata* group is inferred to have had a narrow, pointed flagellomere 1, short proboscis and weak lateral marginal setae on T_{1+2} (Fig. 103). The latter two states are interpreted as symplesiotypies (as discussed above under polarization of states of proboscis length (character 3)), and identify the *S. maculata* group as sister group to the other species groups.

Except for the apotypic shape of flagellomere 1 upon which the *S. maculata* group is based (Figs. 18-22), there are only two synapotypies below the level of species pair.

Therefore relationships within this group are not well understood.

The only resolution is among *S. maculata*, *S. intrudens* and *S. lurida*. The latter two species share four apotypies, clearly attesting to their close phylogenetic relationship. There are a number of differences between *S. intrudens* and *S. lurida*, mostly because of the highly derived condition of the latter.

S. maculata is interpreted as closely related to the *S. intrudens* - *S. lurida* lineage, because of complex modifications of the distiphallus shared between *S. maculata* and *S. intrudens* (characters 13 and 14 (Fig. 102), Figs. 60,62). Since *S. lurida* lacks these modifications (Fig. 63), the plesiotypic states of its distiphallus evidently represent losses (thus the coding of 13-a and 14-a as derived in *S. lurida* in Fig. 103).

Distribution of character states are inadequate to resolve the trichotomy depicted for lineages of the *S. maculata* group (Fig. 103). The autapotypic states of *S. pacifica* result in its general similarity to plesiotypic members of other *Siphona* groups. However, there is no evidence to question placement of *S. pacifica* in the *S. maculata* group.

The phylogenetic position of *S. floridensis* within the *S. maculata* group is also enigmatic. This species has the fewest recognized apotypic states of species analyzed. Therefore, the overall similarity between *S. maculata* and *S.*

floridensis in external characteristics is the result of symplesiotypies, which are unanalyzable cladistically. Also, to consider *S. maculata* and *S. floridensis* as sister species, one must regard the plesiotypic states of the distiphallus in the latter (Fig. 61, cf. Fig. 60) as losses (as inferred for *S. lurida*). Nonetheless, a close relationship between these species is tenable on zoogeographic grounds. A zoogeographic scenerio whereby *S. floridensis* might have evolved from a *S. maculata* population during the Quaternary is outlined in the "Zoogeographic" section. Pending further morphological evidence, I leave the trichotomy in Fig. 103 unresolved.

Two Palearctic species have been identified as members of the *S. maculata* group: *S. collini* Mesnil and *S. efflatouni* Mesnil. They are the only Palearctic *Siphona* species with weak lateral marginal setae on T_{1+2}. They possess an A' type flagellomere 1 and are the only Palearctic species with a short proboscis (not longer than A^2). The distiphallus of *S. collini* has small hooks along the antero-ventral margin (state A'). (Only the female holotype of *S. efflatouni* was examined, so the distiphallus of this species was not studied.) In general habitus *S. collini* and *S. efflatouni* also appear to belong to the *S. maculata* group.

Despite the plesiotypic nature of weak lateral marginal setae on T_{1+2} and a short proboscis, both states are well correlated with the apotypic shape of flagellomere 1 in the

S. maculata group. As such these characteristics are useful indicators of *S. maculata* group members, even though they are interpreted as symplesiotypies.

A test I have not had an opportunity to perform to date involves use of undescribed Oriental *Siphona* species. H. Shima notes (per. comm.) several species similar in appearance to *S. lurida* from the Orient, and study of these would undoubtedly cast light on the phylogeny presented here. It will be particularly interesting to note whether these species are more closely related to *S. lurida* or *S. intrudens*, since the implications critically affect the zoogeographic interpretation as well as the reconstructed phylogeny of the *S. maculata* group.

4.3.3 The S. cristata group

The *cristata* group is based on one apotypic state, shape of flagellomere 1 (Fig. 104).

S. oligomyia is included in this group, though its flagellomere 1 is not characteristic of the group (possessing state 2-A instead of 2-B). Justification for inclusion of *S. oligomyia* in the *S. cristata* group is based on two synapotypies between *S. lutea* and *S. oligomyia*, as discussed below.

At the next higher level on the cladogram (Fig. 104) is shape of distiphallus (state 14-B), uniting the *S. cristata* - *S. multifaria* and *S. lutea* - *S. oligomyia* lineages. Again, *S. oligomyia* does not share the derived state of the other members.

S. pisinnia is treated as sister species to the other species of the *S. cristata* group, though it is actually not as distantly removed phenetically from the rest of the group as it appears in the cladogram. Only three states separate it from *S. multifaria*, and one of these, distiphallus shape (Fig. 65; cf. Fig. 67), is a consequence of the system I employed to delimit states. I have recognized the indentation of the anterior margin of the distiphallus as an apotypic state, while necessarily relegating forms near this shape without an indentation to the plesiotypic state, for lack of distinguishing features. Because of the highly derived appearance of *S. lutea* and *S. oligomyia*, *S. pisinnia* is phenetically closer to *S. multifaria* and some specimens of *S. cristata* than are the others.

Within the *S. cristata* group I have depicted *S. multifaria* and *S. cristata* as sister species (Fig. 104). Under this scheme I have not followed the apparent transformation series of character 6 (colouration), which suggests *S. cristata* is closer to *S. lutea* than to *S. multifaria*. The distiphalli of *S. cristata* and *S. lutea* are also very close (Figs. 66,68). Nevertheless, characters 3 and 7 argue in favour of the depicted arrangement.

Additional support for the reconstruction comes from the Palearctic species *S. flavifrons* Staeger. It is similar in colouration to the yellow form of *S. cristata*, yet probably belongs to the *S. geniculata* group. This is evidence that the B^1 colouration of *S. cristata* need not have shared an ancestry with B^2 colouration of *S. lutea* and *S. oligomyia*.

Character state 6-B^2 is highly apotypic. Through concordance with state 7-A, *S. lutea* and *S. oligomyia* are well established as sister species. *S. oligomyia* is distinctive because of many autapotypic features; had it been of average colouration its species group placement would be uncertain.

A Palearctic species of dubious placement is *S. setosa* Mesnil. It has median marginal setae on T_{1+2}, but none of the other *S. geniculata* group apotypic characteristics. With its 2-B flagellomere 1, it might belong to the *S. cristata* group. Other characteristics are inconclusive: distiphallus type 14-a, proboscis and eye average-sized, colouration average, etc. I leave *S. setosa* unplaced.

Two Palearctic species are easily recognized as members of the *S. cristata* group. One, *S. confusa* Mesnil, has an average-sized eye and proboscis and a flagellomere 1 varied between states A^1 and B^1. The one distiphallus examined is close to state 14-B, but without an indentation anteriorly. A few specimens have a tawny abdomen as in *S. cristata*, while others are of average colouration.

The other Palearctic species, *S. pauciseta* Rondani, has an average-sized to A^1 eye and a proboscis of average length. Flagellomere 1 and distiphallus possess the characteristics of the group, with states 2-B^1 and 14-B.

S. confusa and *S. pauciseta* do not share the apotypic states of *S. lutea* and *S. oligomyia*. Their phylogenetic position relative to *S. pisinnia*, *S. multifaria* and *S. cristata* is unclear. As members of the *S. cristata* group, *S. confusa* and *S. oligomyia* illustrate a deficiency in the distinction between states **A** and **B** of flagellomere 1. These states are not markedly different, and both species indicate that 2-**A** is derivable from 2-**B**. Unfortunately, without additional characters there is no alternative to 2-**B**' as a synapotypy for the group.

S. confusa also illustrates a problem in delimitation of character 14; distiphallus shape. *S. pauciseta* supports recognition of 14-**B** as a good synapotypic state, yet *S. confusa*, like *S. pisinnia*, lacks this state. To incorporate *S. confusa* and *S. pisinnia*, *S. medialis*, *S. floridensis* and *S. pacifica* would also have to be included, thereby considerably reducing the usefulness of this uniquely derived state. A subjective element thus enters the analysis, for resemblance of a type 14-a to a 14-**B** distiphallus is not without significance.

Regardless of the difficulties inherent in recognition of state 14-**B**, it is possible that relegation of *S. pisinnia* to its depicted position is phylogenetically inaccurate. An alternative is to disregard the slight distiphallus differences beween *S. pisinnia* and its relatives, and examine the consequences to the cladogram. A trichotomy results, with the *S. pisinnia* lineage on the same node as the *S. cristata* - *S. multifaria* and *S. lutea* - *S. oligomyia* lineages. Given this possibility, similarity between *S. pisinnia* and *S. multifaria* suggests *S. pisinnia* might be more closely related to the *S. cristata* - *S. multifaria* lineage than to the other. To support this alternative hypothesis (and refute the relationship shown in Fig. 104) a synapotypy is required, and one has not yet been found.

The *S. cristata* group would benefit more than others from analysis of additional characters. Possibilities include larvae, ethological and host data, differences in the reproductive system of females, electrophoresis and cytotaxonomic data. As illustrated above, external features and male genitalia are not particularly amenable to phylogenetic analysis.

4.3.4 The *S. geniculata* group

In North America the *S. geniculata* group includes three species (Fig. 105), one of which (*S. geniculata*), has been introduced by man to this continent. These species share the derived states of one pair median marginal setae on T_{1+2} (albeit not all *S. hokkaidensis* specimens) and a short aristomere 3 (Figs. 28-32).

The apotypic states shared between *S. geniculata* and *S. hokkaidensis* attest to their close phylogenetic relationship, even though most specimens of the latter are without either median marginals on T_{1+2} or a type 2-A' flagellomere 1 (= antennal type 1, Fig. 30).

Five Palearctic species are assignable to the *S. geniculata* group, though their characteristics are varied. Only two species have median marginal setae on T_{1+2}, *S. flavifrons* Staeger and *S. rossica* Mesnil. *S. rossica* is evidently close to *S. hokkaidensis*, with its medium-sized eye and proboscis, a flagellomere 1 near type 2-D, two pair lateral marginal setae on T_3 and a short aristomere 3. I did not have an opportunity to dissect a male specimen, but I predict the male genitalia of this species has a long surstylus.

I recognize *S. flavifrons* as a member of the *S. geniculata* group by its joint possession of median marginals on T_{1+2} (most specimens) and a long surstylus. Its distiphallus is apically truncate, but slightly too wide basally to be classed type 14-C.

S. flavifrons does not have a shortened aristomere 3 and its flagellomere 1 and colouration are as in *S. cristata*. In light of other character state differences I view these similarities as convergences. The characteristic shape of flagellomere 1 for the *S. cristata* group has already been shown to be weakly based. I regard the average-sized aristomere 3 as a significant departure from the condition characteristic of the *S. geniculata* group, for to my knowledge *S. flavifrons* is the only species with median marginals on T_{1+2} and a long surstylus for which the aristomere 3 is not shortened.

S. paludosa Mesnil lacks median marginals on T_{1+2}, but has a short aristomere 3, type 14-B distiphallus and a 15-A surstylus, strongly supporting its placement in the *S. geniculata* group.

I also include two other Palearctic species without median marginals on T_{1+2}, *S. grandistylum* Pandellé and *S. nigricans* (Villeneuve). Both have a flagellomere 1 resembling the 2-D state of *S. hokkaidensis*, and a short aristomere 3. Unfortunately I did not have an opportunity to dissect male specimens of these, which would have provided a good test of their placement.

The only Palearctic species with median marginal setae on T_{1+2} that I exclude from the *S. geniculata* group is *S. setosa* Mesnil. It is discussed under the *S. cristata* group.

I have examined specimens from Ecuador of three undescribed *Siphona* species with median marginal setae on T_{1+2}. In other respects these species are quite unlike members of the *S. geniculata* group (in particular, they lack states 4-A and 15-A), so I exclude them. Discussion of these species and their affinities more appropriately awaits a revision of South American *Siphona* species. I mention them here to demonstrate that not all species with median marginals on T_{1+2} belong to the *S. geniculata* group.

Examined Afrotropical and Oriental *Siphona* species do not have median marginals on T_{1+2} (see world list for species examined).

Despite lack of unequivocal character states for the *S. geniculata* group, concordance among states functions well for distinguishing between included and excluded species. Consideration of Palearctic species illustrates that the *S. geniculata* group is a complex assemblage, yet evidently monophyletic.

4.3.5 The S. futilis group

The apotypic character state for this group is a large eye, best exemplified by the 1-A^{2} state in *S. futilis* and *S. illinoiensis* (Figs. 1,34). Similarity between *S. futilis* and *S. illinoiensis* is such that I can polarize but one difference, length of flagellomere 1.

I cannot with certainty place *S. brunnea* in the *S. futilis* group. In general habitus it resembles *S. futilis* and *S. illinoiensis* despite its autapotypies, so I include *S. brunnea* in this group until such time as its relationship is clarified (Fig. 107).

With *S. brunnea* a provisional member, and only one apotypic (and not unique) state for the group, consideration must be given to states of characters 1, 2 and 14 in placement of non-North American species (Fig. 102).

The Palearctic species *S. boreata* Mesnil might belong to the *S. futilis* group. It has a large eye, average length proboscis (characteristic of the group, but evidently plesiotypic), and average colouration. However, flagellomere 1 is near type 2-F. I did not have an opportunity to study male genitalia of this species, thereby limiting my analysis.

Examined specimens of at least two (possibly undescribed) South American species probably belong to the *S. futilis* group, study of which might help define the group and clarify the position of *S. brunnea*.

4.3.6 The *S. tropica* group

This group is particularly noteworthy because it is well represented in the Afrotropics. Of Afrotropical species examined, *S. unispina* (Mesnil) and *S. gracilis* (Mesnil) are the most easily recognized as members. I hesitate to assign to this group other Afrotropical species, since the characteristics that readily distinguish members in Middle America are widespread among Afrotropical *Siphona* species and not restricted to the *S. tropica* group.

I have used character states of *S. unispina* to help polarize states within the *S. tropica* group. I have assumed the Middle American species to be more closely related among themselves than to *S. unispina*. As a result, states of characters 13 and 14 have been polarized differently than they otherwise would have been (Fig. 106).

In conflict with my understanding of the *S. tropica* group is character state 8-A: setulae on R_1. A single setula is present near bend of R_1 in *S. tropica* and *S. unispina*. Because it is absent from examined specimens of *S. rizaba*, *S. longissima* and *S. akidnomyia*, I suggest it has been independently derived as in other *Siphona* species (*S. lutea* + *oligomyia*, *S. grandistylum*). *S. tropica* could be postulated as closer to *S. unispina* than to the others, but this would not explain the presence of hooks on the distiphallus of *S. longissima* and *S. akidnomyia* (Figs. 76-77), nor their other *S. tropica* group characteristics. Two separate ancestors could be invoked to explain the anomaly, but are not justified on the basis of a single low weight apotypy.

The shared characteristic between *S. longissima* and *S. akidnomyia* is a weak synapotypy. Additional data are needed to elucidate relationships among *S. tropica* group members.

In the Palearctic and Oriental Regions the *S. tropica* group is apparently absent, as it is from the Nearctic Region. In the Neotropics it is most diverse in Middle America. Other than *S. tropica*, I have examined only one species (probably undescribed) of this group from South America (Chile).

The *Siphona* fauna of Middle America is inadequately known. I have examined a single specimen of a new species belonging to the *S. tropica* group that I have not described due to its poor condition. I suspect several other *Siphona* species are undiscovered or undescribed from this region as well.

4.3.7 The S. macronyx group

S. macronyx is placed in a monobasic species group because its phylogenetic position relative to other North American *Siphona* species has not been clarified (Fig. 103).

The large tarsal claws and above average number of setae and setulae on vibrissal angle of *S. macronyx* are derived states shared with *S. lurida* of the *S. maculata* group. This species also has hooks on the distiphallus, a derived state for the *S. maculata, S. floridensis, S. intrudens* and *S. lurida* lineage. Nevertheless, a sister species relationship between *S. macronyx* and *S. lurida* is untenable in light of their overall dissimilarity (Figs. 21,33) and the synapotypies between *S. intrudens* and *S. lurida* (notably a small eye, short proboscis and similar colouration). Furthermore, *S. macronyx* lacks the slender, pointed flagellomere 1, which is apotypic for the *S. maculata* group.

There is a slight similarity between *S. macronyx* and the *S. geniculata* group (characters 2,3 and 9 (Fig. 102)), but *S. macronyx* lacks two of three apotypic states upon which the group is based.

4.4 Evolutionary trends

The most satisfactory method for obtaining information about most characters of varied structure in *Siphona* adults is to observe living specimens under natural conditions. Though I did this intermittently, I did not pursue it intensely. It has been my experience that adults of *Siphona* searching for a mate or host are usually seen fleetingly, and in many instances rarely. On the other hand, adults seeking nourishment can be observed for some time as they probe deeply into flowers with their long proboscises, in quest of nectar. As a result, the functional significance of most derived characteristics can only be gleaned indirectly through study of dead specimens and by analogy with other taxa.

It is a basic tenet in evolutionary studies that most modifications in structure result from selective pressures and have functional significance. If so, the most derived and varied feature of *Siphona* adults, the proboscis, must have attained its present variety because of advantages conferred on its bearers.

The only known function of the proboscis in *Siphona* adults is for procurement of food; chiefly nectar from flowers. Unlike large tachinines, adults of most siphonines are too small to force apart flower components to reach deep nectaries, so the benefits of a long proboscis are obvious. Not only did adults of *Siphona* apparently evolve an elongate prementum and labella to aid feeding, but so too did others, such as adults of certain species of *Ceranthia s. lat.* and *Actia*. Adults of *Clausicella* achieved essentially the same end through elongation of the prementum, albeit with less maneuverability distally than that provided by a geniculate proboscis. In fact, an elongate prementum is found in various groups throughout the Tachinidae, though an elongate labella is apparently unique to the Siphonini.

It is not possible to correlate development of a geniculate proboscis in adult *Siphona* with success of the taxon. For one reason, certain genera like *Ceromya*, *Peribaea* and most species of *Actia* have a short labellar disc, yet approach the diversity of *Siphona*. For another, too little is known about parasite-host interactions to dismiss as minor, developments in that area. However, it is possible that individuals with a long proboscis have a selective advantage over others in varied environments, for they are physically less dependent upon certain kinds of flowers than are their relatives with shorter proboscises. Few *Siphona* species other than members of the primitive *S. maculata* group have a short proboscis, so once attained a long proboscis seems seldom to have shortened (I have inferred just two such reductions; in *S. oligomyia* and *S. akidnomyia*). Therefore a definite trend in adults of *Siphona* species from a short to long proboscis is evident (cf. Fig. 15).

There are no other trends in *Siphona* as unidirectional as that of proboscis length. Greatly varied is eye size, but from the inferred plesiotypic state of an average-sized eye, both small and large eyes are necessarily derived. Shape and size of flagellomere 1 are also considerably varied (even within species), and a trend is not apparent. The significance of varied eye and flagellomere 1 sizes among species is unknown, and speculation is best deferred until more information on behaviour and environment of individual species is available. Within species, males have the larger eye and flagellomere 1, implying both are used in the search for a mate. Females are probably mostly host oriented, and the slightly longer palpus of females in most species might be involved in determining host suitability.

Notable in the evolution of *Siphona* species is the similarity among species groups in mean number of apotypic states (Fig. 102). Though the *S. maculata* group is interpreted as the most primitive, two included species (*S. intrudens* and *S. lurida*) are very derived, so even this group is not markedly removed from the others in degree of apotypy. This pattern implies that evolution within *Siphona* has progressed at a relatively constant rate, without invasion of, and diversification in, new adaptive zones.

5. ZOOGEOGRAPHIC CONSIDERATIONS

5.1 Diversity and general patterns

I prefer not to use terms Nearctic and Neotropical in discussing New World *Siphona* species distributions. Most Middle American *Siphona* species are not derived from extant Nearctic or South American species groups. To emphasize this point I discuss distribution patterns in terms of America north of Mexico, Middle America and South America. Only two species are not confined within boundaries of one of these areas. *S. pisinnia* (Fig. 83) ranges widely in America north of Mexico and Middle America. The distribution of *S. tropica* (Fig. 101) extends into extreme northwestern South America, but for present purposes will be regarded as a Middle American species.

My use of terms Palearctic, Oriental and Afrotropical are defined in the preamble to "World list". I treat *S. geniculata* as a Palearctic species in the ensuing discussion because in North America it is an introduced species.

The 79 described *Siphona* species[5] are distributed as follows, by region in order of decreasing diversity:

Afrotropical - 40 species.

Palearctic - 17 species.

America north of Mexico - 14 species.

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[5] excluding *S. maculipennis* Meigen, an unrecognized Palearctic species that is probably conspecific with a recognized species.

Middle America - 7 species.
South America - 3 species.
Oriental - 3 species.

Madagascar is included in the Afrotropical Region. It has three endemic species and five others that are shared with the mainland. The Canary Islands off the northwest coast of Africa, with endemic species *S. seyrigi*, is considered Palearctic. So too is Africa north of the Sahara, from whence *S. nigricans* was described (from Algeria).

Between America north of Mexico and the Palearctic Region four species (excluding introduced species *S. geniculata*) are known to be shared: *S. cristata*, *S. hokkaidensis*, *S. lurida* and *S. maculata*. The Palearctic Region is not known to share species with any other region. America north of Mexico has *S. pisinnia* in common with Middle America.

The *Siphona* fauna of South America is inadequately known. I estimate from the little material I have examined from the region at least ten species live there, possibly more.

I have examined adults of one undescribed species of *Siphona* from Australia. *Siphona* species from the Oriental Region are not well known and are probably more diverse than indicated by three described species.

In the previous section a cladistic analysis helped define six North American *Siphona* species groups. Within each group there is a general pattern of geographic distribution involving at least two regions. Three general interregional patterns are recognizable among the five groups:

1) America north of Mexico - Palearctic Region

This pattern is evidenced by a close relationship between species of both regions, with a high proportion of Holarctic distributions for species with northern records (three of six New World species). Representing this pattern are the *S. maculata*, *S. cristata* and *S. geniculata* groups.

2) America north of Mexico - Middle America

Here belongs the *S. futilis* group, wherein closely related *S. illinoiensis* and *S. futilis* are in adjacent regions. There is evidently a closer affinity to the fauna of South America than the Old World, but this has not been firmly established.

3) Middle America - Afrotropical Region

In the New World the *S. tropica* group is most diverse in Middle America. No species have been assigned to the group from America north of Mexico or the Palearctic Region. Although represented by at least one species in South America, the zoogeographically most significant relationship is between Middle American and African members of the group.

Within North America another set of distribution patterns, those involving species rather than species groups, is evident. To a large extent these reflect biotic changes that have taken place in the region since the Middle Tertiary. These are:

1) Transcontinental (mostly cool to cold temperate) - *S. cristata*, *S. hokkaidensis*, *S. intrudens*, *S. lutea*, *S. maculata*, *S. medialis* and *S. multifaria*.
2) Western - *S. geniculata* (introduced), *S. lurida*, *S. macronyx*, *S. oligomyia*, *S. pacifica* and *S. pisinnia*.
3) Eastern - *S. floridensis* and *S. illinoiensis*.
4) Mexican - *S. akidnomyia*, *S. brunnea*, *S. futilis*, *S. longissima*, *S. rizaba* and *S. tropica*.

5.2 Historical zoogeography

It is premature to speculate in detail about historical events responsible for present day *Siphona* species distributions in North America. The three main distribution patterns identified in the previous section make obvious the fact that the North American assemblage of *Siphona* species is polyphyletic. Indeed, interregional relationships are so complex that the monobasic *S. macronyx* group is the only one that is exclusively North American.

The best zoogeographic hypothesis is one that stems from a thorough cladistic analysis of a group. Only then are all requirements of a scientific hypothesis met: explanatory power, internal consistency, predictive power and testability (falsification) (Ball, 1976; Noonan, 1979). As a consequence the cladograms in Figs. 103-107 (representing only North American species) are inadequate for detailed interpretation of the historical zoogeography of North

American *Siphona* species.

Siphona species groups, on the other hand, are suitable for zoogeographic analysis because they are based on inclusive and not (as for North American species) exclusive data. *Siphona* species groups are monophyletic units, members of which need not be cladistically arranged for the groups to be zoogeographically analyzed, provided regional group relationships are known (Hennig, 1966b). For instance, the very close phylogenetic relationships among taxa of the *S. maculata* group between America north of Mexico and the Palearctic Region are indicative of past faunal exchange between regions. This presumed interchange satisfies the four requirements of a scientific hypothesis, so a zoogeographic analysis seeking a historical explanation for the interchange is well founded.

Ideally all *Siphona* species groups and data about intergroup affinities should be included in a zoogeographic treatment of the genus. It may be many years before sufficient information on *Siphona* cladistics is gathered to realize this goal. Therefore I judge it timely to interpret aspects of *Siphona* history from the data available now.

In the absence of a fossil record there is an alternative means for deriving age of a taxon. The minimum age is that of the earliest demonstrable vicariant event within the taxon. Maximum age is that already determined for a higher taxon to which the taxon in question belongs, or as evidenced by the taxon's global distribution pattern (provided taxon is widespread). For the Calypteratae in general the early fossil record is inadequate; they have been assumed pre-Tertiary in age for many years (eg. Rohdendorf, 1974), but not until 1970 was the first calypterate fly from the Mesozoic (Upper Cretaceous, 70 mybp[1]) recorded (McAlpine, 1970). To date a fossil tachinid has not been discovered that has a significant bearing on age of origin of this family (van Emden, 1959), much less *Siphona*.

It has become possible in the past decade to outline in a broad sense major geologic and climatic events of the earth since early Mesozoic time. Concomitant with this knowledge has developed a general willingness on the part of biogeographers to interpret species distributions according to established geologic and climatic theory. Fossils remain valuable means of hypothesis testing, but are no longer central to most biogeographical analyses unless the fossil record is unusually complete. Recent studies of Diptera reflect this trend. For example, Bowden (1973) suggests a Late Cretaceous origin of *Dischistus* (Bombyliidae) based on distributional data. Papavero (1977), places origin of the Oestridae between Late Jurassic and Early Cretaceous on the basis of a Gondwanian distribution. Most remarkable is McAlpine's (1977) documentation of a Gondwanian distribution for an extant piophilid genus, *Protopiophila* (the first Gondwanian distribution recognized in a genus of the Schizophora).

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[1] million years before present.

By analogy with studies on other Schizophora the family Tachinidae is apparently pre-Tertiary in origin. As long as distributional data suggest a more recent origin of *Siphona* than analogy has for the Tachinidae, then there is no age conflict between them'.

Although *Siphona* species are cosmopolitan, they show no sign of a Late Cretaceous or earlier origin. Had *Siphona* evolved in the Southern Hemisphere during the Late Cretaceous a Gondwanaland distribution would be expected (assuming extinction was not a factor). By Late Cretaceous Africa was drifting north, while South America, Antarctica and Australia were still connected via at least an archipelagic route (Dietz and Holden, 1970; Smith, Briden and Drewry, 1973; Howarth, 1981). In fact, the southern route through Antarctica may have been in use by terrestrial animals as late as Early Oligocene (Raven and Axelrod, 1975).

An adequately supported argument against a Gondwanaland distribution for *Siphona* must await a cladistic analysis of African, South American and Australian species. However, the few *Siphona* species in South America and especially Australia, relative to Africa and the northern continents, suggests dispersal of *Siphona* species was not taking place between southern continents in the Late Cretaceous.

'as yet a time scale has not been proposed for origin of tachinid subfamilies and tribes, so these taxa cannot be discussed here.

In the Northern Hemisphere during the Late Cretaceous, high sea levels had a greater isolating effect on continents than did plate positions. Across the North Atlantic and through Beringia, land (?filter) bridges were apparently in operation, though north-south seaways hindered intracontinental faunal movements (Kurtén, 1969; Hallam, 1973; Matthews, 1979; Howarth, 1981).

If *Siphona* species were in the Northern Hemisphere during the Late Cretaceous I would expect a more pronounced difference between *Siphona* faunas of America north of Mexico and the Palearctic Region than evident in the *S. maculata*, *S. cristata* and *S. geniculata* groups. Presumably *Siphona* species could have dispersed readily between northern regions had they been there during the late Cretaceous. Yet present faunal similarities are better explained by Late Cenozoic exchange.

Based on available evidence and without comparable studies within the Tachinidae, I hypothesize a maximum age of *Siphona* as Late Cretaceous. As mentioned earlier, minimum age necessarily precedes the earliest demonstrable vicariant event. Before discussing how I apply this principle to *Siphona*, it is appropriate to consider region of origin of the genus. This simplifies the discussion further on.

I emphasize I am discussing *region* of origin, not *center* of origin. Thus I am not concerned with the controversy between centers of origin in the Darwinian sense and vicariance biogeography (Croizat *et al*., 1974). In a region of continental size, taxa can evolve under either paradigm and produce equal diversity, so the difference is not important here.

Siphona probably arose in the Old World. The basis for this inference is twofold. First, Old World *Siphona* species and species of siphonines related to *Siphona* (*Actia*, *Ceromya* and *Peribaea* spp.) outnumber New World taxa by a wide margin. Secondly, an invasion of North America from the Old World during the Tertiary by *Siphona* is compatible with New World species distributions, while it is inconceivable without a number of assumptions that invasion of *Siphona* into the Palearctic Region from North America would lead to the present patterns of diversity and distribution in the Old World.

To account most parsimoniously for Old World *Siphona* patterns, Africa must be interpreted as region of origin for the genus. Diversity favours this choice, but does not negate the possibility of adaptive radiation in Africa and an origin elsewhere. More important than diversity is the pattern of diversity, as determined through comparison of species numbers among regions.

An African origin of *Siphona* is compatible with the observed decrease in number of species from a high in the Afrotropical Region to a low in the Oriental and Australian Regions.

If the Palearctic Region were postulated as area of origin of *Siphona*, the observed pattern of diversity would be quite unparsimonious. During most of the Tertiary, Africa was isolated from other regions by the Tethys Sea (Cooke, 1972; Hallam, 1973; Howarth, 1981). It is unlikely Palearctic *Siphona* individuals crossed this barrier enough times to attain the present Afrotropical diversity in number of species and species groups without similarly invading the more accessible Oriental Region.

Returning to the question of minimum age of *Siphona*, I limit my analysis to species groups in which cladistic relationships between regions have been determined. These are the *S. maculata*, *S. cristata*, *S. geniculata* and *S. tropica* groups. The first three do not reflect a necessarily old distribution pattern. The *S. tropica* group is disjunct between Middle America and Africa, and it is from this group I hypothesize minimum age of *Siphona*.

Concomitant with historical biogeographic hypotheses are assumptions. Assumptions should be formalized, for they enhance the central hypothesis by clearly distinguishing the assumed from the inferred (cf. Lewis, 1980: 554). Furthermore, while some assumptions are untestable (and are, for that reason, assumptions) others result from insufficient data and become falsifiable as new data are added. Assumptions of the latter type should be accompanied by statements concerning their testability, to make the central hypothesis more scientific.

Assumptions upon which I base my analysis of the disjunction of the *S. tropica* group between Middle America and Africa are:

1) The cladistic relationship between Middle American members of the *S. tropica* group and *S. unispina* in Africa (Zaire) has been correctly interpreted. (Falsifiable by cladistic study of additional taxa or reinterpretation of existing data.)

2) Members of the *S. tropica* group in South America are derived from Middle American species; they are not Gondwanaland relicts. (Relationships testable by cladistic analysis.)

3) Africa was region of origin of *Siphona* and the *S. tropica* group. (Subject to corroboration or refutation through study of world species groups and (for *Siphona*) closely related genera.)

4) Disjunction in distribution of the *S. tropica* group is not a result of long distance dispersal between Middle America and Africa. The dispersal ability of *Siphona* adults is attested to by their presence on islands: Madagascar, Canaries, Juan Fernández, Tierra del Fuego, Philippines and others. There are eight species recorded from Madagascar, of which five are shared with Africa. Presumably the Mozambique Channel (500km wide) has not been an efficient barrier to dispersal of *Siphona* individuals. There is no evidence, however, that individuals cross wide barriers. For example, *Siphona* is not recorded from Hawaii. I suspect water gaps are more easily crossed than other physical or climatic barriers.

5) Current hypotheses of paleoclimate and paleogeography relevant to my interpretation of past events are accurate. (Testable by results of future research.)

6) Climate and habitat requirements of *S. tropica* group taxa have not changed significantly throughout their existence. (Discovery of a *S. tropica* group species in a cold temperate environment would cast doubt on this assumption.)

An explanation is sought that accounts for the geographically disjunct nature of the *S. tropica* group. Assuming the genus originated in Africa subsequent to the Late Cretaceous, direct dispersal across the Atlantic is considered improbable because South America and Africa were widely separated by that time. The only available land route was northward to Europe or Asia and into North America through Beringia or across a North Atlantic land or filter bridge.

First consider the ecological aspects involved in a Northern Hemisphere route. The *S. tropica* group is now restricted to the Tropics, so existence of northern land bridges is not sufficient to account for *Siphona* migration into North America. Had a *S. tropica* group taxon invaded the Northern Hemisphere from Africa during a relatively cool period, descendants would presumably still be there. If instead there was a period of significant warming in the north, a *S. tropica* group taxon could have entered Eurasia and spread to North America without a major shift in way of life. If deterioration of the warm trend took place soon after the ancestral New World *Siphona* taxon arrived in North America, then retreat to Middle America could have occurred without leaving northern, cool adapted descendants. These events could not have occurred later than the Early Oligocene (34 mybp) (Wolfe, 1978, as Late Eocene).

For many years the Geoflora[1] concept dominated paleobotanical interpretations. Paleocene and Eocene climates of northern North America were interpreted as subtropical to warm temperate with gradual cooling from the Oligocene to Quaternary (Dorf, 1964). The Geoflora concept has recently come under incisive criticism with the realization that plant species respond individualistically to climatic shifts (Graham, 1972; Wolfe, 1978). Nowhere is this better exemplified than in late Quaternary macrofossil records of packrat middens (Wells, 1979; Van Devender and Spaulding, 1979).

Recent studies substantiate a warm period from Middle Eocene to Early Oligocene but envision much warmer conditions than the Geoflora model, followed by rapid climatic deterioration (Wolfe, 1978; Matthews, 1979). Paratropical[2] conditions are thought to have prevailed at higher latitudes over most of the Northern Hemisphere (Wolfe, 1978; Matthews, 1979). During this period the most suitable conditions of the Tertiary must have existed for entry of a *S. tropica* group taxon into North America.

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[1] a Geoflora is a flora that undergoes little compositional change over a long period of time.
[2] intermediate to tropical and subtropical

Physical aspects of a *S. tropica* group taxon dispersing from Africa into Eurasia and then to North America prior to Early Oligocene is complicated by two factors. First, the Tethys Sea isolated Africa from Eurasia during most of the Tertiary, such that faunal exchange was primarily limited to brief periods of (?filter) connection in the Late Oligocene, Late Miocene and Late Pliocene (Cooke, 1972; Hallam, 1973). It is not precluded that other connections of very short duration occurred during which time *Siphona* could have entered Eurasia. Alternately, *Siphona* might have crossed the water barrier directly, by chance dispersal (a sweepstake route; recall Madagascar fauna). By whatever means a *S. tropica* group taxon reached Eurasia, timing was apparently not coincident with a period of substantial mammalian exchange. More important to my hypothesis than *Siphona* crossing the Tethys Sea at the most opportune time is a *S. tropica* group taxon reaching the climatic corridor before it closed in the Early Oligocene.

The second complication pertaining to a *Siphona* taxon reaching North America is the Turgai Strait separating Europe and Asia during the Early Tertiary (Adams, 1981). *Siphona* could have entered Europe by a route through Gilbraltar and crossed a North Atlantic land bridge (Matthews, 1979) without ever reaching Asia. Conversely, dispersal could have been *via* Asia and Beringia. The latter route would be corroborated by discovery of a relict *S.*

tropica group species in the Oriental Region.

Subsequent to the Early Oligocene, the climate in northern regions cooled rapidly (Wolfe, 1978, as "terminal Eocene event"). Because *S. tropica* group taxa are not known from America north of Mexico or the Palearctic Region, I suggest they were unable to adapt and so moved southward as conditions changed. This movement could have been in response to shifts in hosts' ranges, but I doubt this. Even though *Siphona* hosts are inadequately known, the general distribution pattern of *Siphona* species - habitation of islands and continents far and wide - suggests to me that hosts are ubiquitous and not crucial to the understanding of *Siphona* zoogeography.

It is unfortunately premature to attempt to cover circumstances by which the *S. tropica* group became established in Middle America since hosts, habitats and other aspects of extant species' way of life are unknown. Habitat information is vital, for the history of Tertiary floras is complex (Axelrod, 1975, 1979; Rosen, 1978). It is significant, however, that the *S. tropica* group is not represented in eastern North America. Apparently the *S. tropica* group did not become associated with the temperate rain forest widely distributed in the United States and Middle America by the Middle Tertiary (Graham, 1972; Axelrod, 1975, 1979).

Little data are available for inference of the history of the *S. maculata*, *S. cristata* and *S. geniculata* groups in the Old World. The former is recognized as the most primitive *Siphona* species group, so it presumably arose in Africa prior to all others. Examined specimens of *Siphona* taxa from Africa did not include *S. maculata* group members, so the group may have been virtually replaced in that region by more derived taxa. In America north of Mexico the *S. maculata*, *S. cristata* and *S. geniculata* groups have the same pattern of distribution, so probably have similar histories there. These histories are explored.

Species distributions are primarily northern and western in America north of Mexico, and from this several inferences can be drawn. It is likely the *S. maculata*, *S. cristata* and *S. geniculata* groups have not had a long history in the New World. The distributional pattern does not indicate an Eocene to Early Oligocene association with paratropical conditions as shown in the *S. tropica* group. Neither are eastern relicts of the Middle Tertiary temperate rain forest evident.

Members of the *S. maculata* and *S. cristata* groups were probably first to enter North America, and did so since Late Miocene through Beringia[10]. By then a distinctive flora associated with Upper Tertiary orogenies was developing in the west, while drier conditions were experienced in central regions and the temperate rain forest was retreating eastward and southward (Graham, 1972).

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[10] North Atlantic land bridge(s) broken by that time (Matthews, 1979).

A Late Miocene or younger *Siphona* invasion of North America might account for certain western elements in the distribution patterns of the *S. maculata* and *S. cristata* groups. The notion that North Pacific taxa are younger than taxa in eastern United States was also reached by Iwatsuki (1972) based on distribution of bryophytes.

It is possible both *S. pacifica* and *S. pisinnia* (or their ancestors) represent Late Miocene - Early Pliocene associations with young Rocky Mountain environments, particularly with their inferred status as primitive members of the *S. maculata* and *S. cristata* groups, respectively. The latter might be the older, for its distribution implies a warm temperate to subtropical adaptation. Neither species seems to represent a center of origin for North American members of its group, so I infer that subsequent migrations of *S. maculata* and *S. cristata* group taxa from the Palearctic Region took place.

A western distribution of possibly more recent age is that of *S. oligomyia*. As sister species to *S. lutea*, it almost certainly arose in America north of Mexico. *S. lutea* is cool temperate in adaptation and transcontinental in distribution (Fig. 89), and it is apparently parapatric or narrowly sympatric with the range of the more southerly distributed *S. oligomyia* (Fig. 90). Southward shifts in range of *S. lutea* (or ancestor) during Pleistocene glaciations perhaps lead to a vicariance of parental range in the west, with new species, *S. oligomyia*, developing a unique set of adaptations and structural characteristics.

As mentioned in the "Phylogenetic interpretation" section, the relationship between *S. maculata* and *S. floridensis* is cladistically unresolved (Fig. 103), though these species might represent sister species, as inferred from their geographic distributions.

S. maculata is widespread across northern North America (Fig. 82), while *S. floridensis* is only recorded from Florida and adjacent areas. Assuming *S. maculata* reached North America prior to the Holocene, it would have experienced a southward displacement during Pleistocene glaciations.

Under full glacial conditions of the Wisconsin (18,000ybp) (or an earlier glaciation), *S. maculata* might have reached northern Florida, as did some other boreal and cool temperate elements of the biota (reviewed in Wright, 1981). Florida was apparently too dry to support mesic forest during the Wisconsin full-glacial, but xeric oak-pine forest was present (Watts and Stuiver, 1980). Whatever the exact nature of the biotas, community structures must have been unique.

Perhaps as the Laurentide ice sheet retreated and the climate warmed, most populations of *S. maculata* migrated northward, while others became stranded in pockets of suitable habitat in the south. Though most of the latter became extinct, *S. floridensis* might be a living descendant of one population that managed to survive and adapt as conditions changed. (Similarly, apparently disjunct populations of *S. maculata* in Nevada and southern Colorado (Fig. 82) might also be relicts of the once extensive southern range of this species, though they have not undergone the phenetic change of *S. floridensis*.)

Considerable similarity between North American and Palearctic members of the *S. maculata* and *S. cristata* groups indicate faunal exchanges have continued into the Quaternary period. At least three species in common between regions almost certainly reflects Pleistocene exchange during interglacials.

The *S. geniculata* group as well could have entered North America as early as Late Miocene, but there is no indication of this. *S. medialis* is more southerly distributed than *S. hokkaidensis* and more atypical of the group, so its arrival in North America presumably predates that of *S. hokkaidensis*. I interpret the extraordinarily varied appearance of *S. hokkaidensis* as primarily a Quaternary phenomenon, whereby populations were isolated and diverged. Further consideration of this taxon must await study of Palearctic members.

The relationship between *S. futilis* and *S. illinoiensis* of the *S. futilis* group is very close, but other *S. futilis* group affinities are nebulous. Perhaps the group is very old; in the New World as old or older than the *S. tropica* group, since cool temperate taxa are evidently lacking.

As sister species, *S. futilis* and *S. illinoiensis* conform to a distributional pattern of noted zoogeographic importance (Martin and Harrell, 1957; Axelrod, 1975; Rosen, 1978; Allen and Ball, 1980). *S. futilis* and *S. illinoiensis* are, respectively, found in Mexico (Fig. 96) and eastern United States (Fig. 92). It is generally agreed, on the basis of abundant data, that very little biotal exchange has occurred between Mexico and eastern United States since the Miocene, when the Neotropical corridor between these areas deteriorated (Martin and Harrell, 1957; Rosen, 1978; Allen and Ball, 1980). The corridor was apparently not re-established even during Pleistocene full-glacials; at least not with mesic forest elements (reviewed in Wright, 1981).

Despite the apparent rarity of post-Miocene biotal exchange between Mexico and eastern United States, I am reluctant to propose a Miocene vicariance for *S. futilis* and *S. illinoiensis*. By analogy with diversification of the *S. tropica* group in Mexico and inferred recent vicariances of *S. lutea* and *S. oligomyia*, and *S. maculata* and *S. floridensis*, a time span of ca. 15 or more million years for the vicariance (without major change) of *S. futilis* and *S. illinoiensis* seems too long. A more recent (Pleistocene) vicariance or dispersal is suggested by phenetic evidence. If this explanation is valid, this example is one of the few that demonstrates a post-Miocene connection between Mexico and eastern United States for mesic adapted taxa.

Siphona affinities between Middle and South America have not been closely examined. Most species appear derived from northern elements, with a few evidently autochthonous species. I expect exchange prior to the Pliocene connection of North and South America occurred, though infrequently, leading to a small endemic *Siphona* fauna in South America.

To reiterate, the following are the main conclusions drawn from a historical zoogeographic analysis of species groups and North American species of *Siphona*:

1) *Siphona* originated in Africa since the Late Cretaceous,
2) a *S. tropica* group taxon entered North America through a northern paratropical corridor connecting the Old and New Worlds before the climate cooled in Early Oligocene,
3) minimum age of *Siphona* is Early Oligocene,
4) the *S. maculata*, *S. cristata* and *S. geniculata* groups entered North America via Beringia since the Late Miocene and periodic exchange continued into the Pleistocene, and
5) three species pairs represent Pleistocene vicariant events: *S. maculata* and *S. floridensis*, *S. lutea* and *S. oligomyia*, and *S. futilis* and *S. illinoiensis*.

The major historical zoogeographic events concerning *Siphona* species within North America are summarized in Fig. 108.

One of the elements of a zoogeographic hypothesis founded in part on cladistic relationships is its predictive power (Ball, 1976). Explicit predictions, like assumptions, contribute to the clarity and significance of hypotheses.

The assumptions listed earlier are testable and therefore render their own predictions. To those can be added another. I do not expect taxa belonging to the *S. maculata*, *S. cristata* and *S. geniculata* group to be found in South America, for I interpret the ancestors of North American members of these groups northern in origin and temperate to cold temperate in adaptation. Thus, representation of one or more of these groups in South America would imply either an earlier incursion into North America than I hypothesized (ie. during a warm period) or a shift in adaptation of a member taxon from temperate to subtropical or tropical.

6. CONCLUDING REMARKS

It should be apparent from the foregoing text that much remains to be learned about the genus *Siphona*. The basic classificatory work is inadequate for such regions as South America, Australia and the Orient, and until the required studies have been completed, it will continue to hinder attempts such as mine to delve into the historical (phylogenetic and zoogeographic) aspects of the genus.

With few unique and reliable character states of adults by which to distinguish *Siphona* species, identifications are commonly difficult. Since most keys are based exclusively on morphological differences among species, only discovery of new morphological characters are likely to improve them. Nevertheless there are other avenues of investigation into which I have not ventured that might prove useful for species delimitation and phylogenetic analysis. These include larval characters, host records, electrophoresis and cytological characters.

I have written little about the ecological requirements of *Siphona* species, for indeed there is little known. Hosts are unrecorded for most North American species and additional information (such as habitat preferences) is similarly lacking. I can but hope others will examine these aspects of *Siphona* species that I have not.

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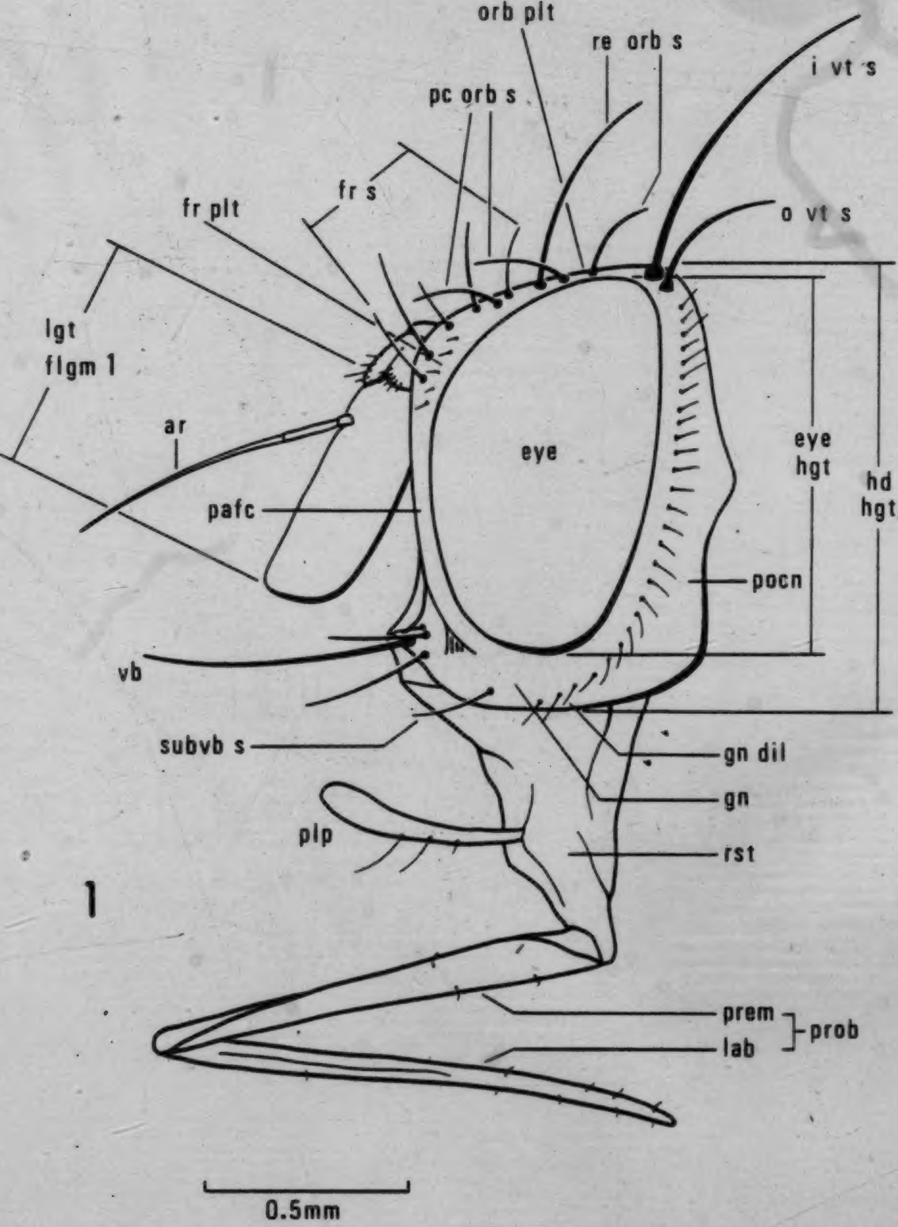
FIGURES

Fig. 1. Terms and measurement of *Siphona* head features. Head profile of male *S. illinoiensis*.

Abbreviations: ar, arista; eye, compound eye; eye hgt, eye height; fr plt, frontal plate; fr s, frontal setae; gn, gena; gn dil, genal dilation; hd hgt, head height; i vt s, inner vertical seta; lab, labella; lgt flgm 1, length of flagellomere 1; orb plt, orbital plate; o vt s, outer vertical seta; pafc, parafacial; pc orb s, proclinate orbital setae; plp, palpus; pocr, postcranium; prem, prementum; prob, proboscis; re orb s, reclinate orbital setae; rst, rostrum; subvb s, subvibrissal seta; vb, vibrissa.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gn dil
gn
plp
rst
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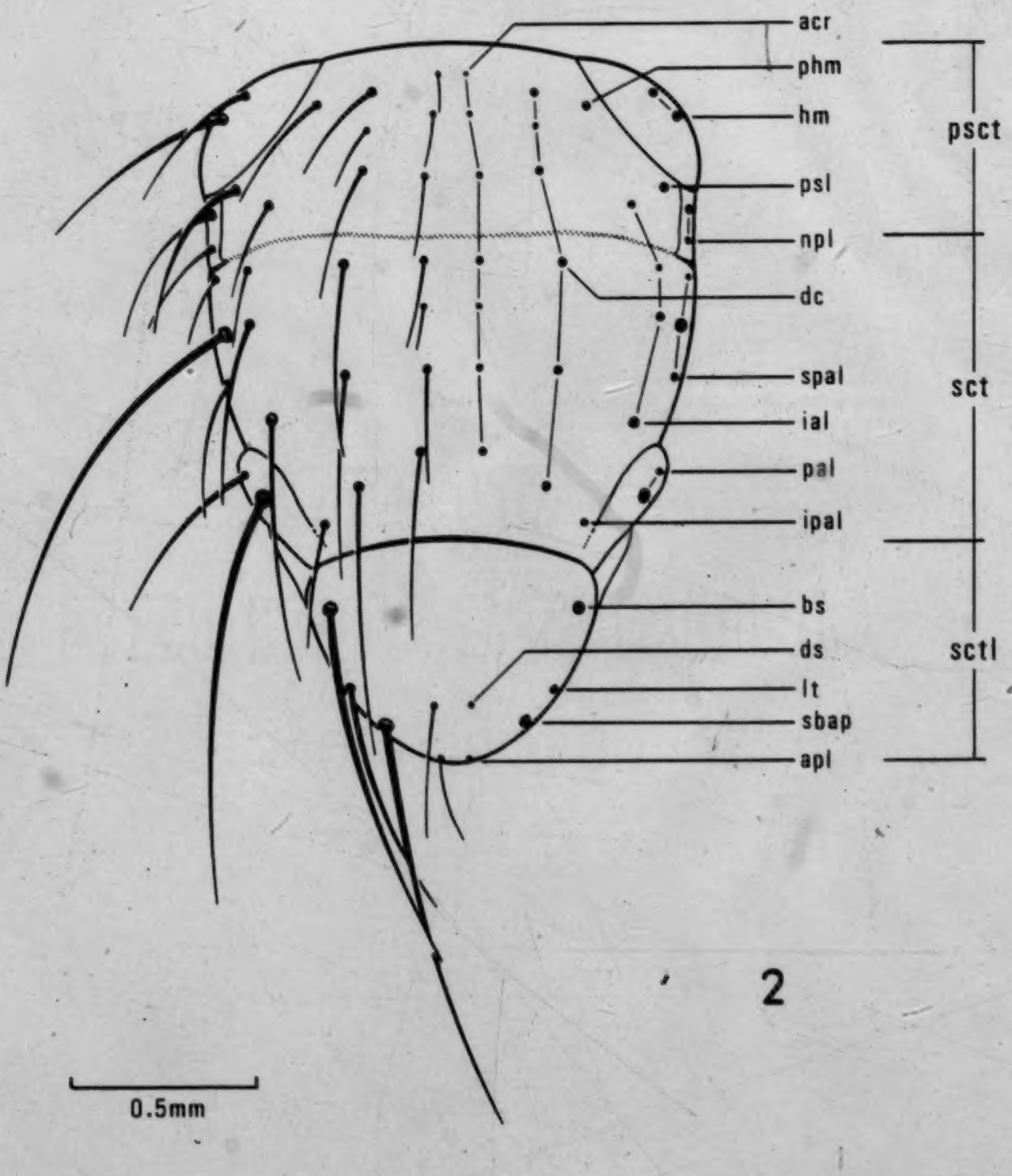
0.5mm

1

Fig. 2. Structure and terms of *Siphona* thoracic nota, as illustrated by *S. macronyx*.

Abbreviations: *Notal divisions:* psct, prescutum; sct, scutum; sctl, scutellum. *Setae:* acr, acrostichal; apl, apical; bs, basal; dc, dorsocentral; ds, discal; hm, humeral; ial, intra-alar; ipal, intrapostalar; lt, lateral; npl, notopleural; pal, postalar; phm, posthumeral; psl, presutural; sbap, subapical; spal, supra-alar.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0.5mm

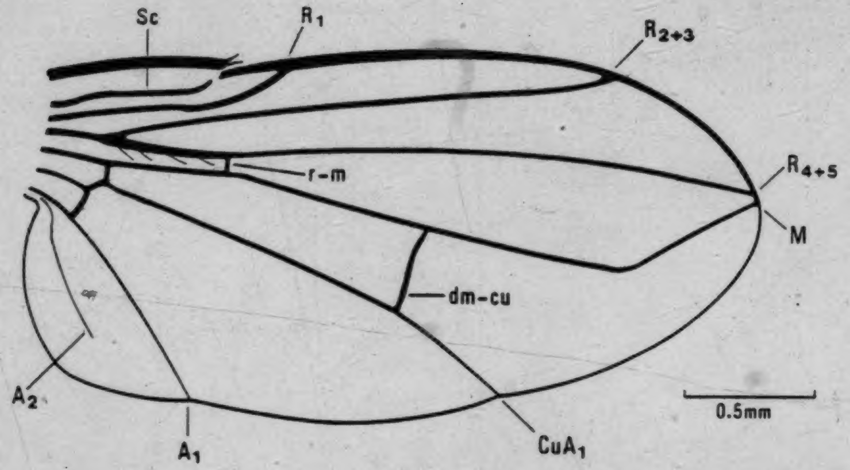
2

Fig. 3. Right wing of *S. maculata*, illustrating average bristling on R_{4+5} and *Siphona* venation.

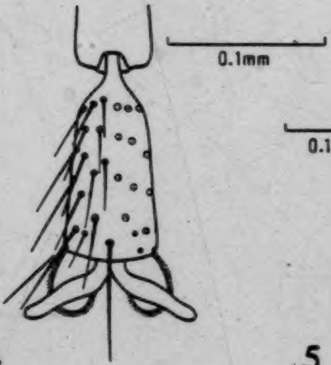
Figs. 4-6. Male foreleg acropods, dorsal aspect. Setae shown on one side only. Claw hooks directed ventrally, hence not visible in figures. Figs. 4 and 6 illustrate average-sized claws and pulvilli, Fig. 5 large claws and pulvilli. Fig. 4. *S. illinoiensis*. Fig. 5. *S. intrudens*. Fig. 6. *S. lutea*.

Figs. 7-8. Preabdomens, dorsal aspect. [Median marginal setae foreshortened in figures; subequal in length to laterals.] Fig. 7. *S. intrudens*, illustrating weak marginal setae and absence of median marginal setae on T_{1+2}. Fig. 8. *S. medialis*, illustrating strong lateral marginal setae and presence of median marginal setae on T_{1+2}.

Abbreviations: *Veins:* A_1, A_2, branches of anal; CuA_1, cubitus; M, media; R_1, R_{2+3}, R_{4+5}, branches of radius; Sc, subcosta. *Crossveins:* dm-cu, discal medial-cubital; r-m, radial-medial. *Abdomen:* lat marg, lateral marginal seta; med marg, median marginal seta; T_{1+2}, T_3, T_4, T_5, abdominal terga.


Sc
R_1
R_{2+3}
r-m
R_{4+5}
M
dm-cu
A_2
A_1
CuA_1
0.5mm

3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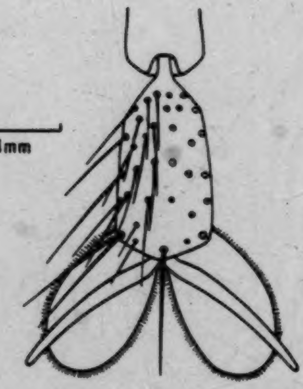
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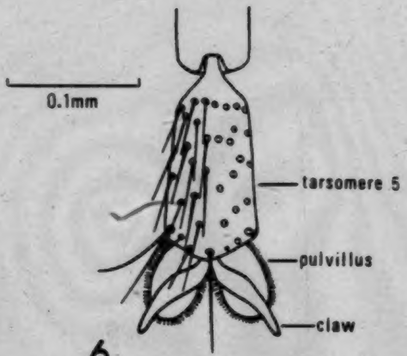
5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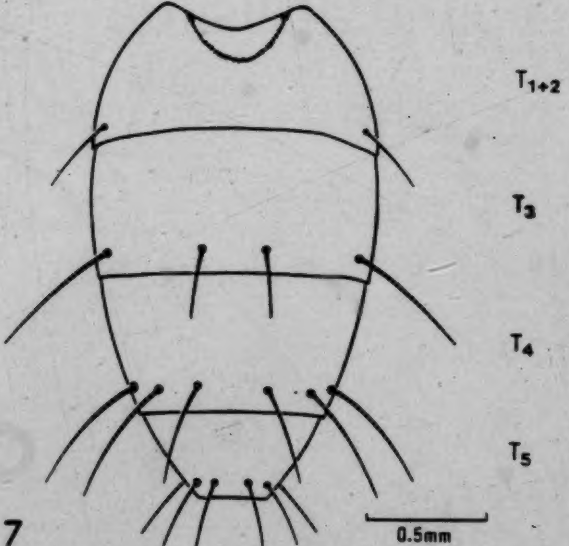
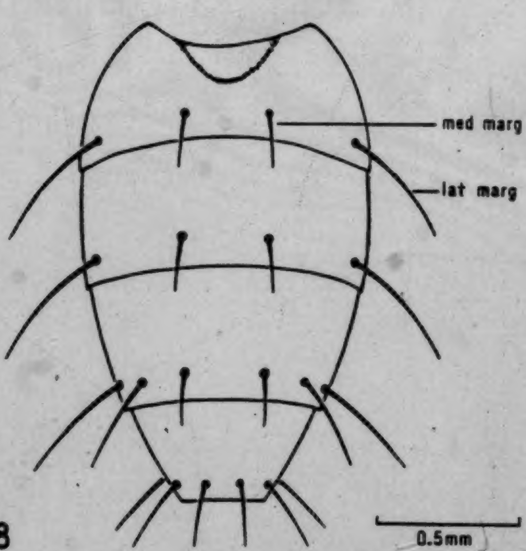
tarsomere 5
pulvillus
claw

6


T_{1+2}
T_3
T_4
T_5
0.5mm

7


med marg
lat marg
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8

Fig. 9. Structure and terms of *Siphona* male genitalia, as illustrated by *S. illinoiensis*. Fig. 9a. Anterior view of distiphallus. Fig. 9b. Lateral view of genitalia.

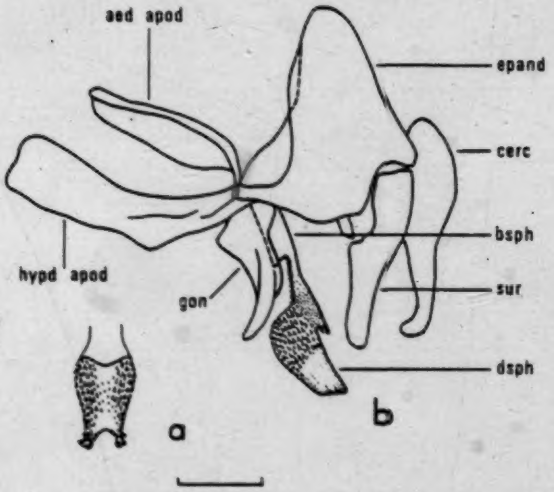
Fig. 10. Sternum 5 of *S. lutea*, illustrating average condition of postero-lateral margins.

Fig. 11. Sternum 5 of *S. oligomyia*, illustrating hooked condition of postero-lateral margins.

Fig. 12. Structure and terms of *Siphona* female genitalia, as illustrated by *S. hokkaidensis*. Fig. 12a. Ventral view. Fig. 12b. Dorsal view. Fig. 12c. Lateral view.

Abbreviations: *Male genitalia:* aed apod, aedeagal apodeme; bsph, basiphallus; cerc, cerci; dsph, distiphallus; epand, epandrium; gon, gonite; hypd apod, hypandrial apodeme; sur, surstylus. *Female genitalia:* cerc, cerci; sg 8, segment 8; st 5, 6, 7 and 10, abdominal sterna.

Scale bars = 0.1mm.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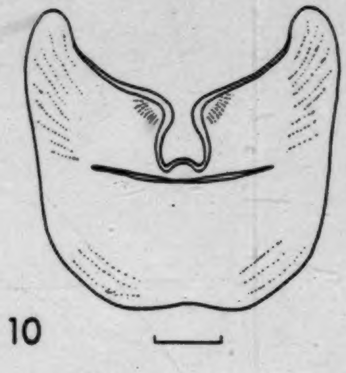
9



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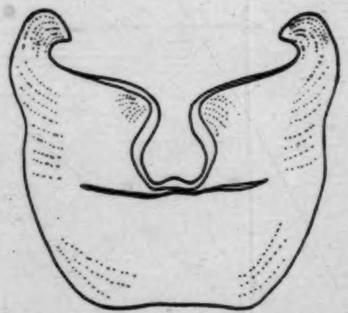

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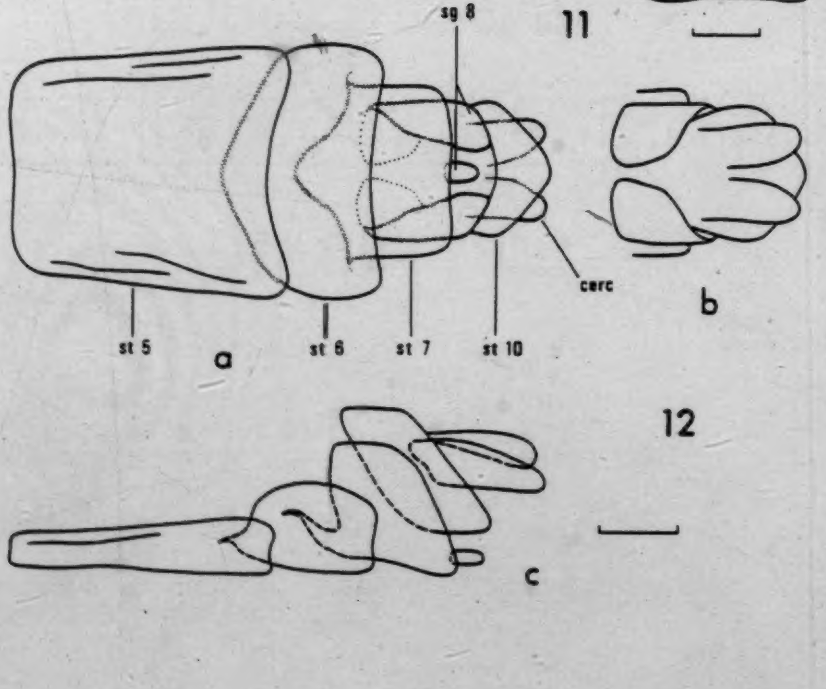
sg 8
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st 10
a
b
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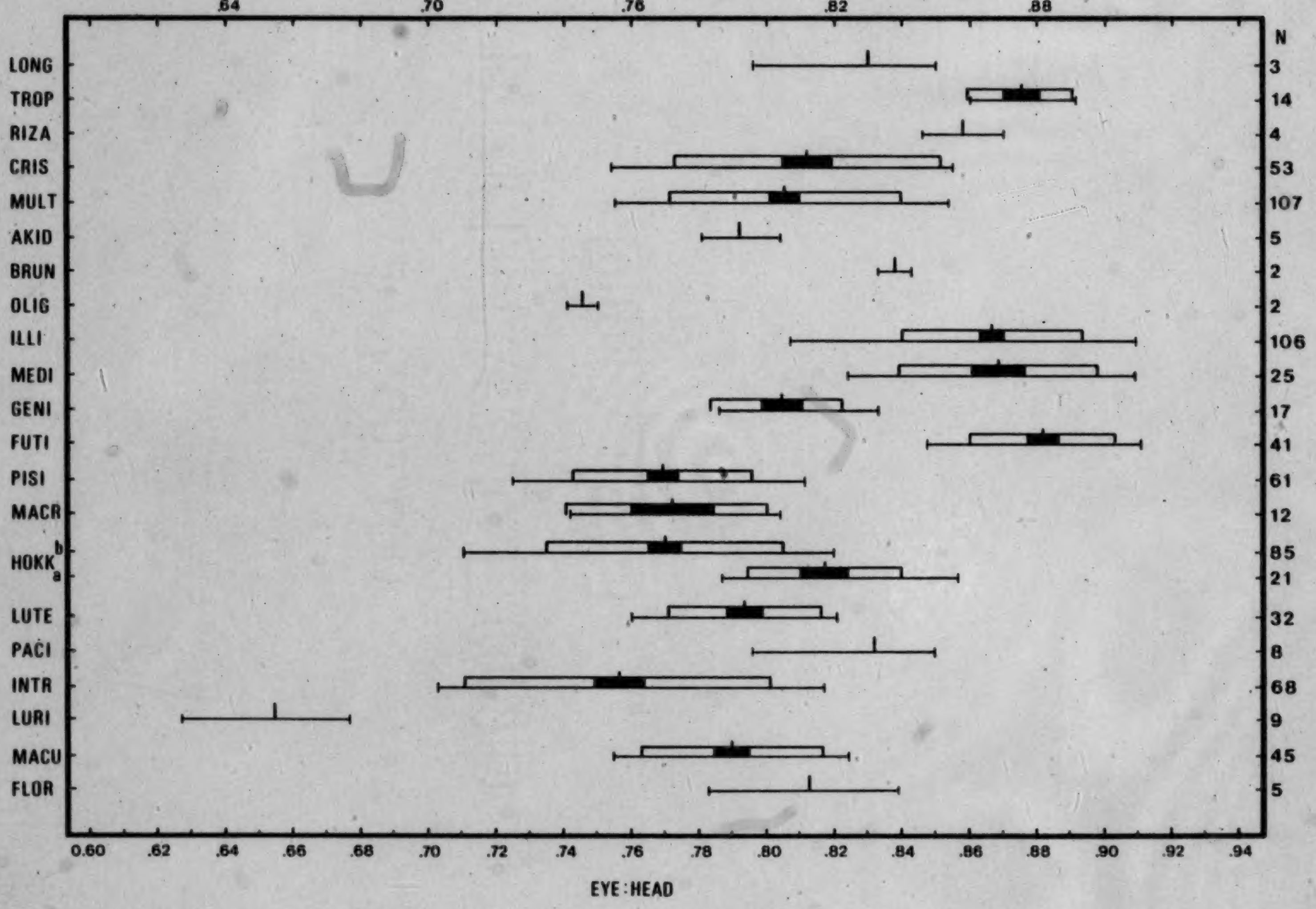
12

Fig. 13. Hubbs-Hubbs diagram illustrating variation among specimens of *Siphona* species; eye height: head height. The range for each species is indicated by a horizontal line and the mean by a short vertical line. A hollow rectangle represents two standard errors to either side of the mean and a solid rectangle represents 1.5 standard deviations to either side of the mean. Only range and mean values are shown for samples with less than ten specimens. See "Methods" section for further information.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N
LONG 3
TROP 14
RIZA 4
CRIS 53
MULT 107
AKID 5
BRUN 2
OLIG 2
ILLI 106
MEDI 25
GENI 17
FUTI 41
PISI 61
MACR 12
HOKK b 85
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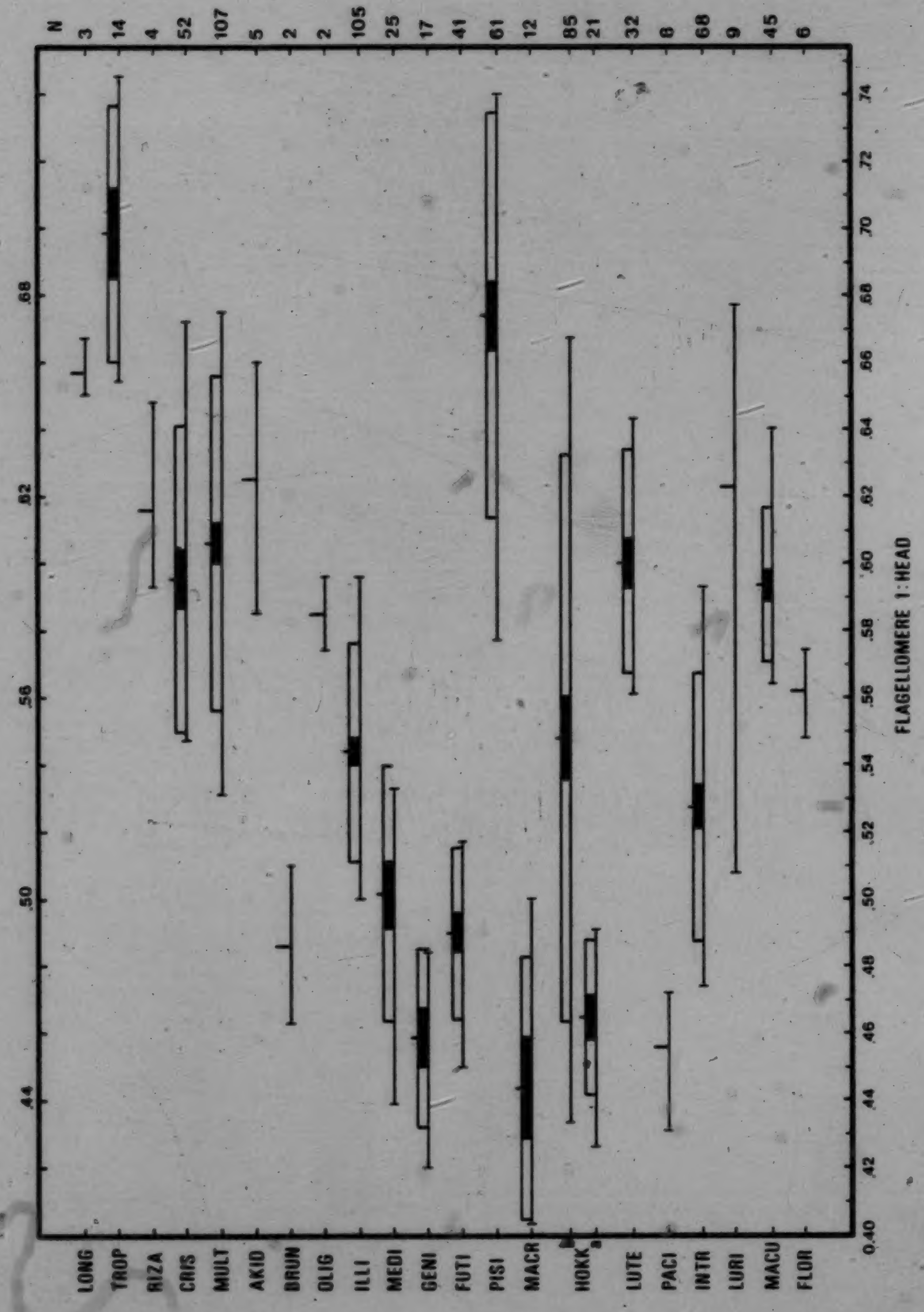
LUTE 32
PACI 8
INTR 68
LURI 9
MACU 45
FLOR 5
0.60
.62
.64
.66
.68
.70
.72
.74
.76
.78
.80
.82
.84
.86
.88
.90
.92
.94
EYE:HEAD

Fig. 14. Hubbs-Hubbs diagram illustrating variation among specimens of *Siphona* species; length of flagellomere 1: head height. See caption for Fig. 13 and "Methods" section for further information.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TROP 14
RIZA 4
CRIS 52
MULT 107
AKID 5
BRUN 2
OLIG 2
ILLI 105
MEDI 25
GENI 17
FUTI 41
PISI 61
MACR 12
HOKK 85
HOKK 21
LUTE 32
PACI 8
INTR 68
LURI 9
MACU 45
FLOR 6
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.56
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.62
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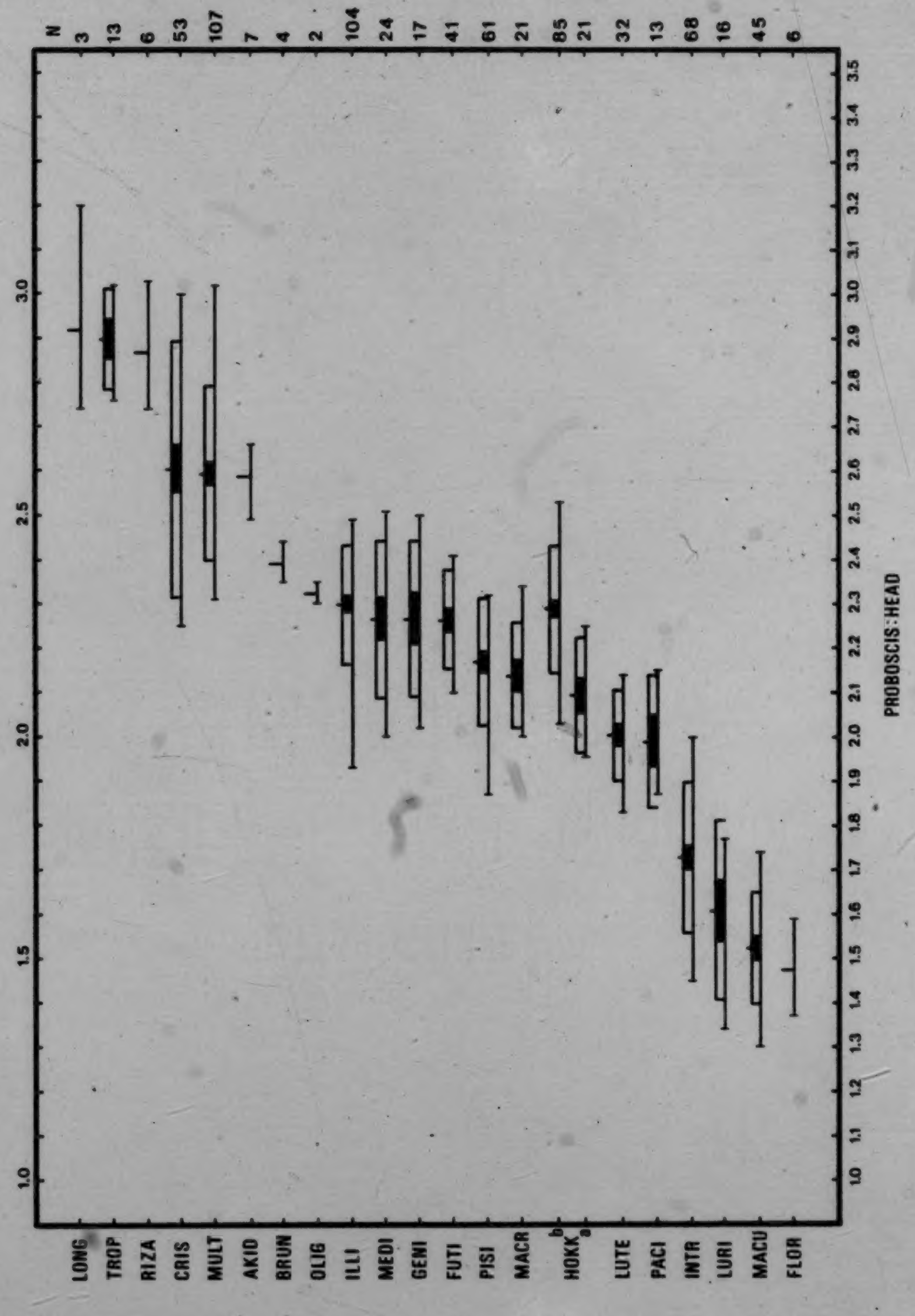
.66
.68
.70
.72
.74
FLAGELLOMERE 1:HEAD

Fig. 15. Hubbs-Hubbs diagram illustrating variation among specimens of *Siphona* species; proboscis length: head height. See caption for Fig. 13 and "Methods" section for further information.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TROP 13
RIZA 6
CRIS 53
MULT 107
AKID 7
BRUN 4
OLIG 2
ILLI 104
MEDI 24
GENI 17
FUTI 41
PISI 61
MACR 21
HOKK b 85
HOKK a 21
LUTE 32
PACI 13
INTR 68
LURI 16
MACU 45
FLOR 6
1.0
1.5
2.0
2.5
3.0
1.0 1.1 1.2 1.3 1.4 1.5 1.6 1.7 1.8 1.9 2.0 2.1 2.2 2.3 2.4 2.5 2.6 2.7 2.8 2.9 3.0 3.1 3.2 3.3 3.4 3.5
PROBOSCIS:HEAD

Fig. 16. Hubbs-Hubbs diagram illustrating variation among specimens of *Siphona* species; length of flagellomere 1: eye height. See caption for Fig. 13 and "Methods" section for further information.

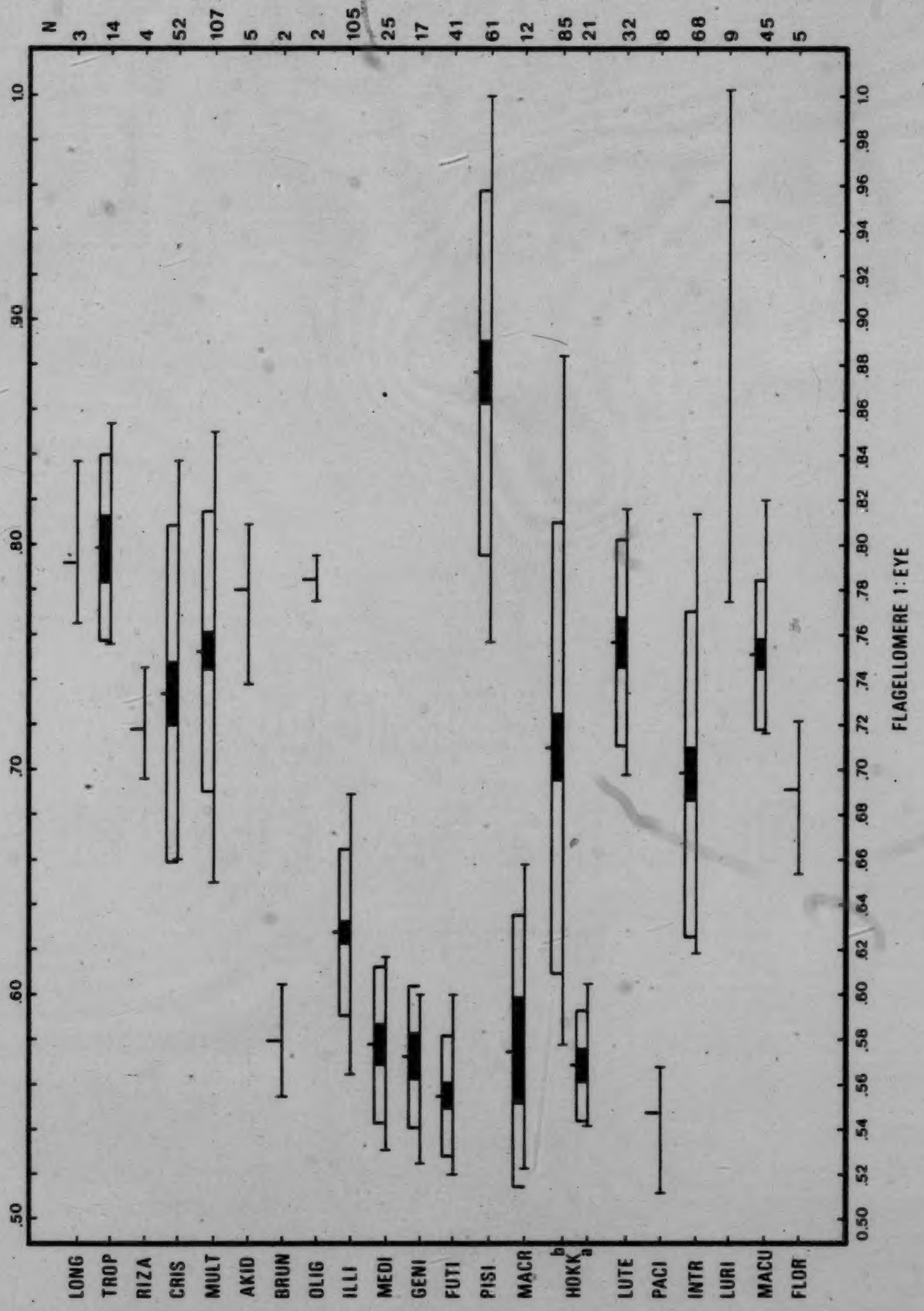
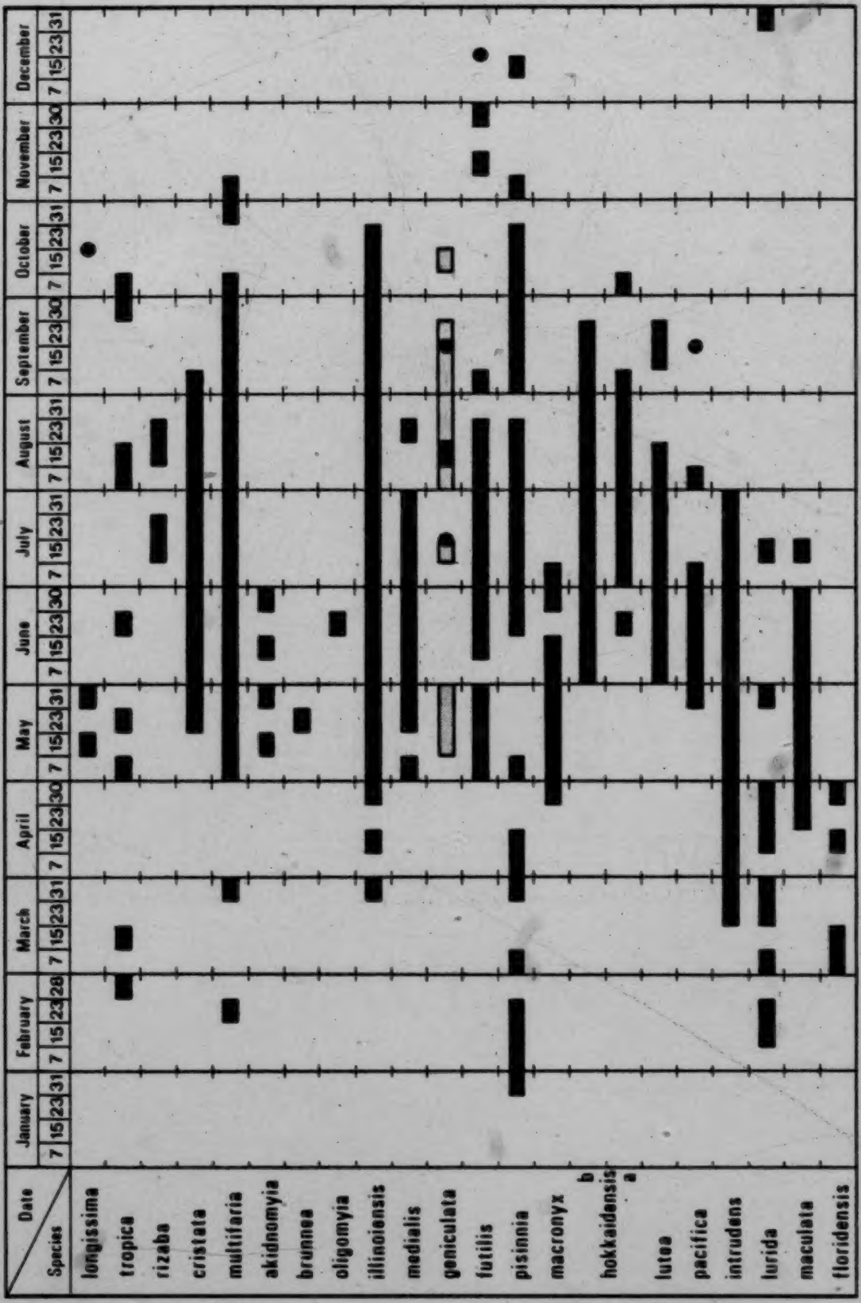

N
LONG 3
TROP 14
RIZA 4
CRIS 52
MULT 107
AKID 5
BRUN 2
OLIG 2
ILLI 105
MEDI 25
GENI 17
FUTI 41
PISI 61
MACR 12
HOKK b 85
HOKK a 21
LUTE 32
PACI 8
INTR 68
LURI 9
MACU 45
FLOR 5
.50
.60
.70
.80
.90
1.0
0.50 .52 .54 .56 .58 .60 .62 .64 .66 .68 .70 .72 .74 .76 .78 .80 .82 .84 .86 .88 .90 .92 .94 .96 .98 1.0
FLAGELLOMERE 1: EYE

Fig. 17. Chart of adult seasonal occurrence of *Siphona* species, based on dates of collection. Solid rectangles signify at least one adult specimen was collected during period indicated. A dot represents a date record for which month only was available. The lightly stippled rectangles shown for *S. geniculata* signify data taken from European specimens.


Date
Species
January
February
March
April
May
June
July
August
September
October
November
December
7
15
23
31
28
30
longissima
tropica
rizaba
cristata
multifaria
akidnomyia
brunnea
oligomyia
illinoiensis
medialis
geniculata
futilis
pisinnia
macronyx
hokkaidensis
a
b
lutea
pacifica
intrudens
lurida
maculata
floridensis

Figs. 18-21. Male head profiles of *Siphona* species.

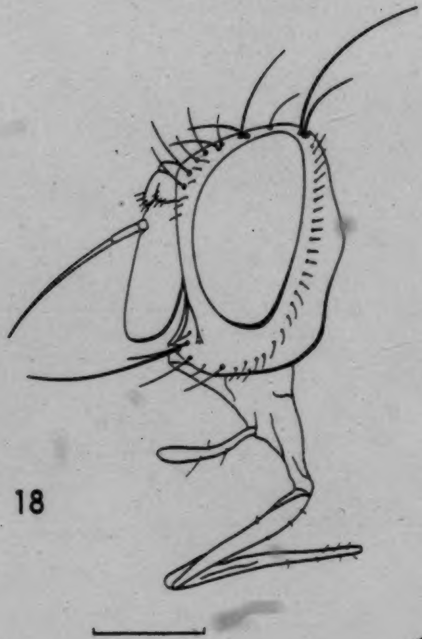
Fig. 18. *S. maculata*.

Fig. 19. *S. floridensis*.

Fig. 20. *S. intrudens*.

Fig. 21. *S. lurida*.

Scale bars = 0.5mm.



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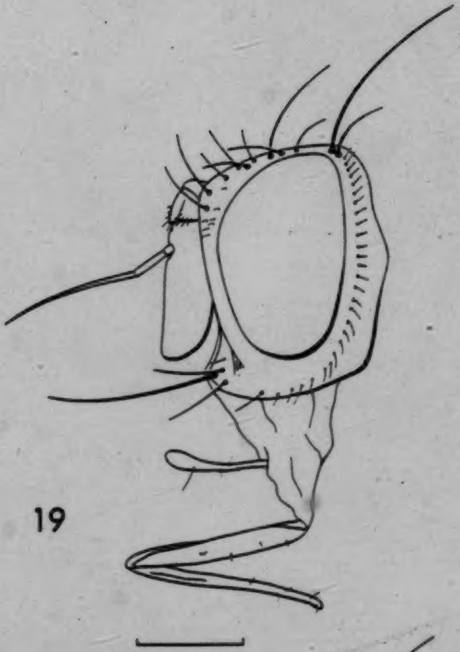

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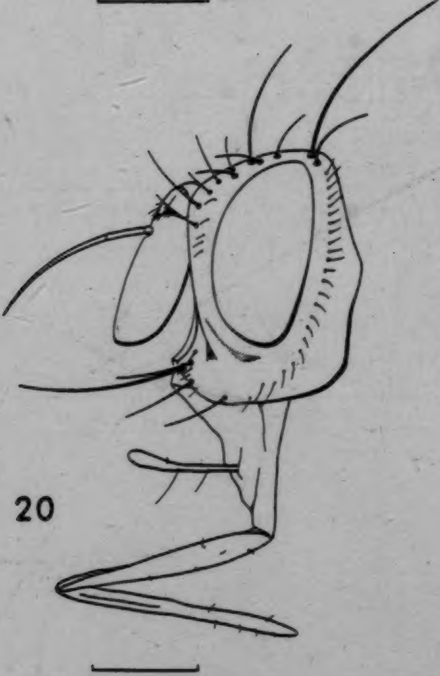

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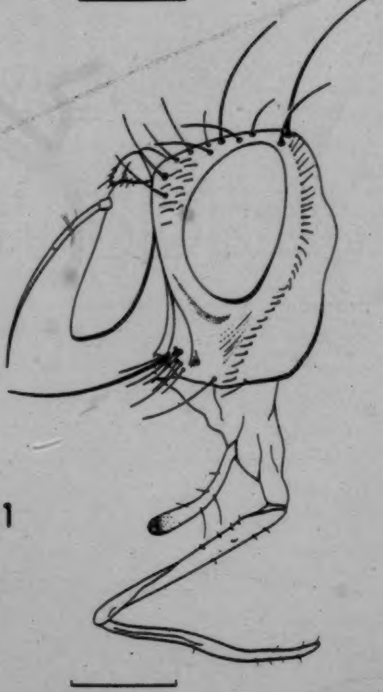

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Figs. 22-25. Male head profiles of *Siphona* species.

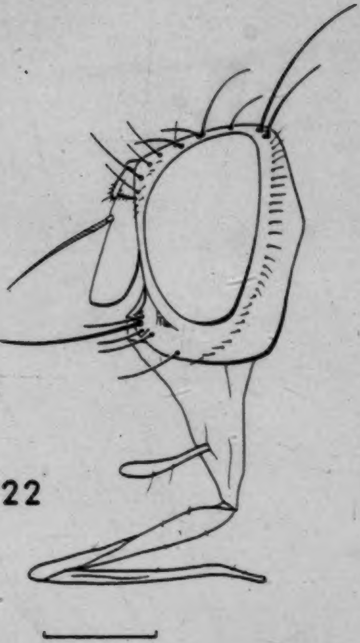
Fig. 22. *S. pacifica*.

Fig. 23. *S. pisinnia*.

Fig. 24. *S. cristata*.

Fig. 25. *S. multifaria*.

Scale bars = 0.5mm.



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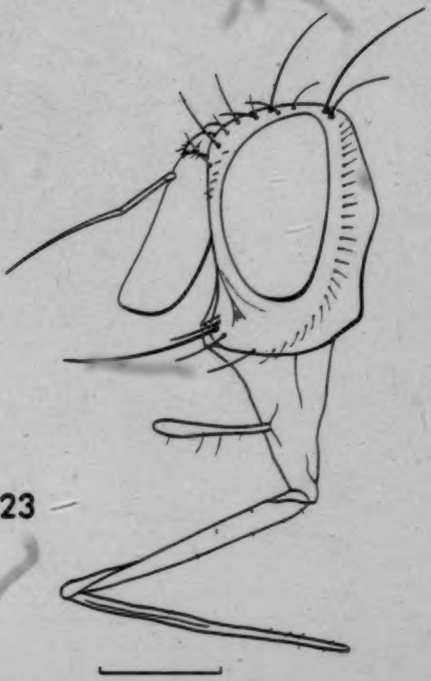

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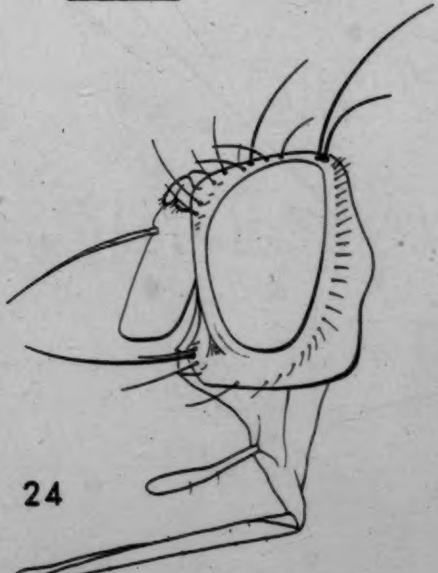

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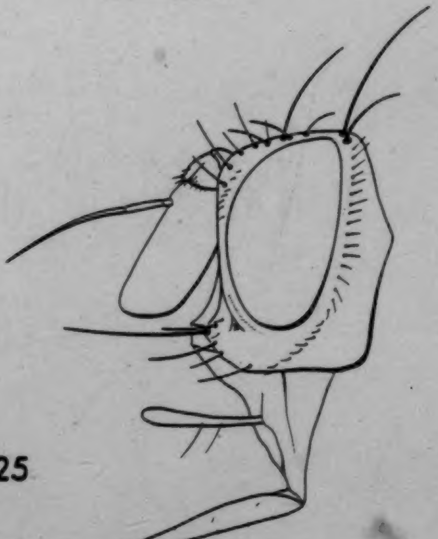

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Figs. 26-29. Male head profiles of *Siphona* species.

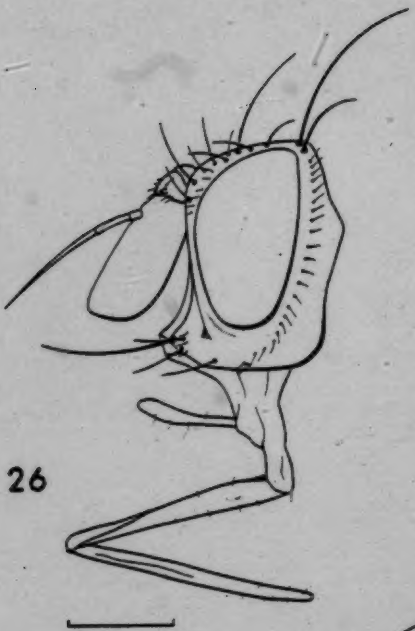
Fig. 26. *S. lutea*.

Fig. 27. *S. oligomyia*.

Fig. 28. *S. geniculata*.

Fig. 29. *S. medialis*.

Scale bars = 0.5mm.



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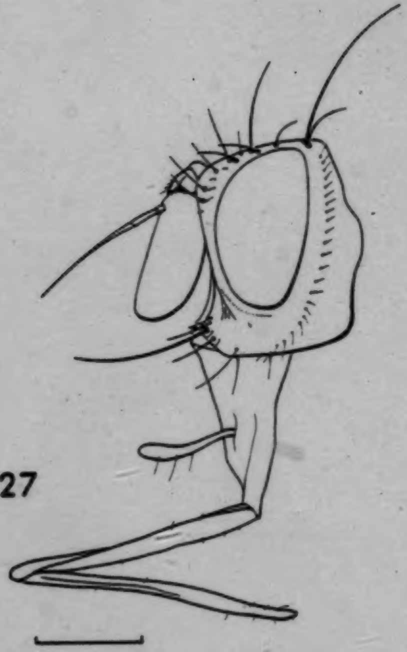

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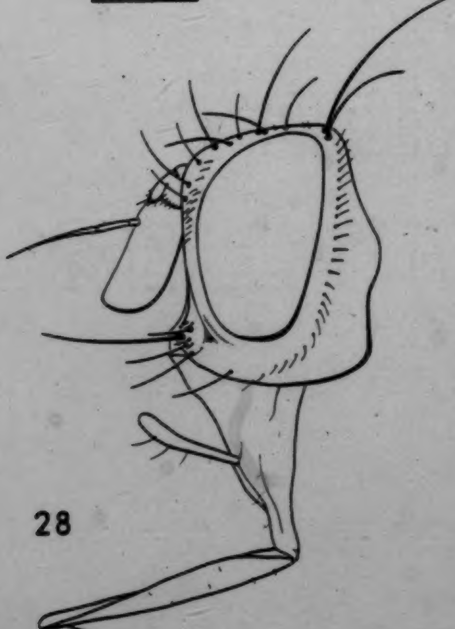

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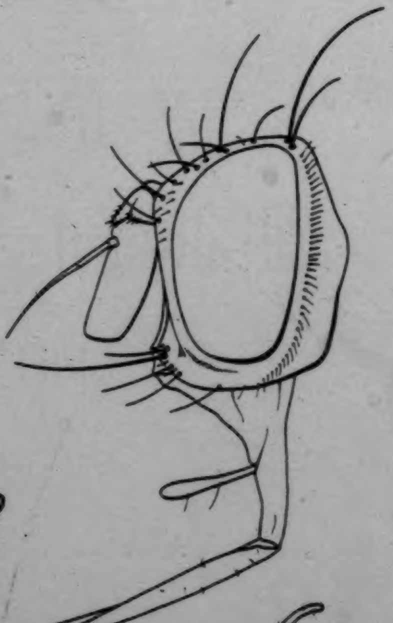

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Figs. 30-33. Male head profiles of *Siphona* species.

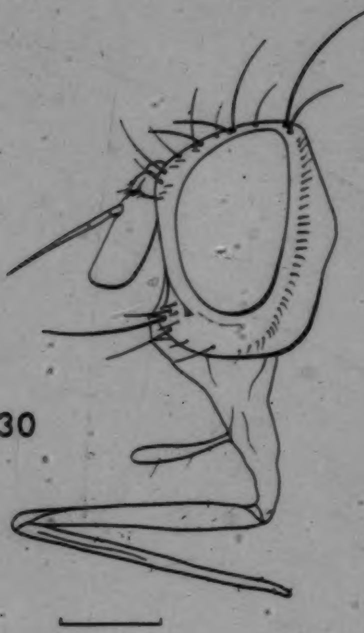
Fig. 30. *S. hokkaidensis*, antennal type 1.

Fig. 31. *S. hokkaidensis*, antennal type 2.

Fig. 32. *S. hokkaidensis*, antennal type 3.

Fig. 33. *S. macronyx*.

Scale bars = 0.5mm.



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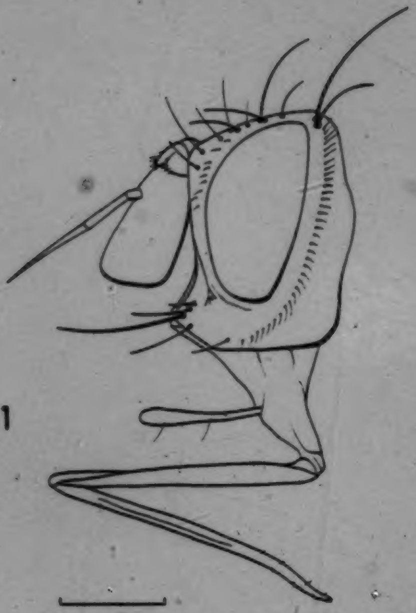

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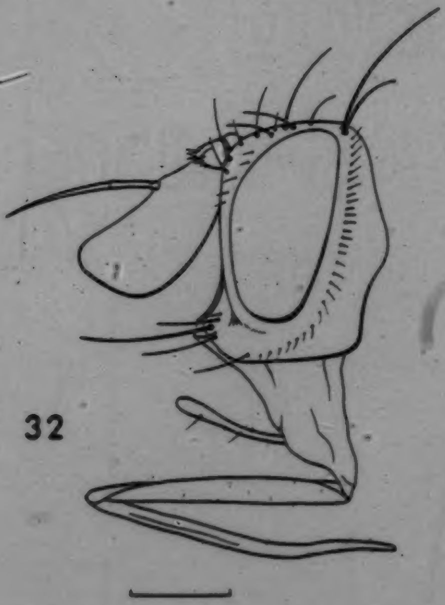

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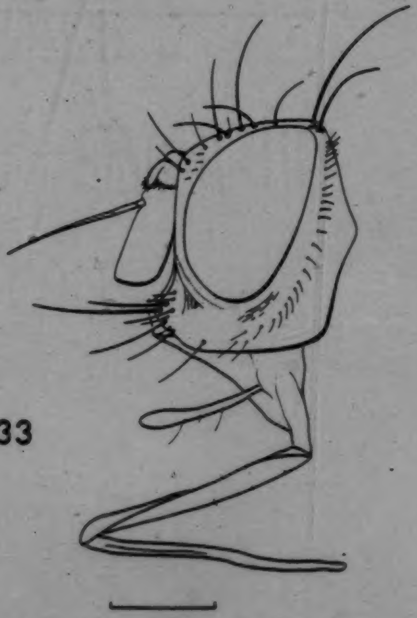

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Figs. 34-37. Male head profiles of *Siphona* species.

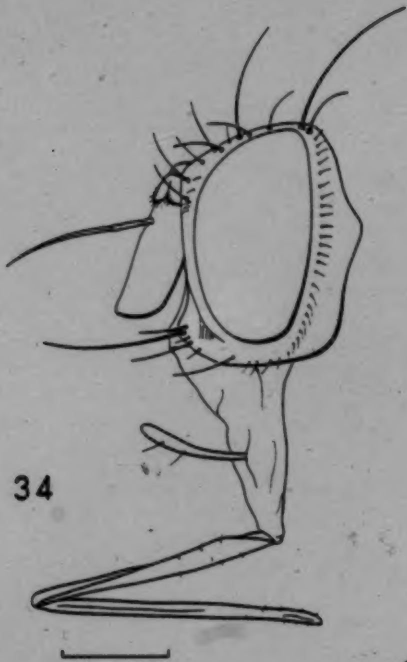
Fig. 34. *S. futilis*.

Fig. 35. *S. brunnea*.

Fig. 36. *S. akidnomyia*.

Fig. 37. *S. longissima*.

Scale bars = 0.5mm.



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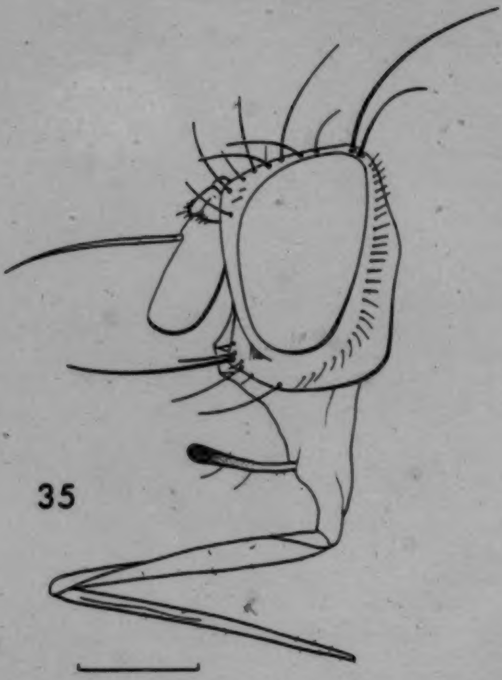

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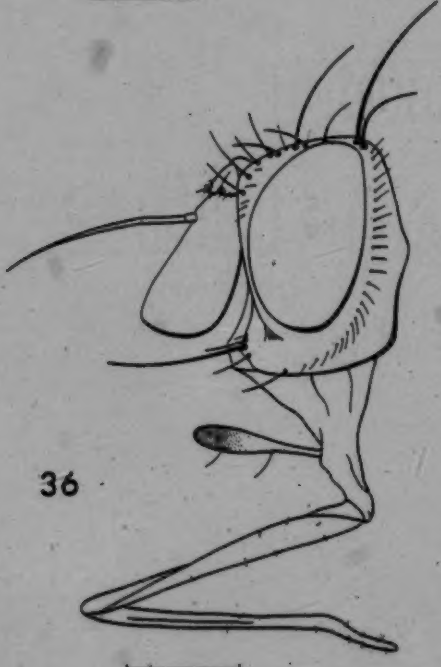

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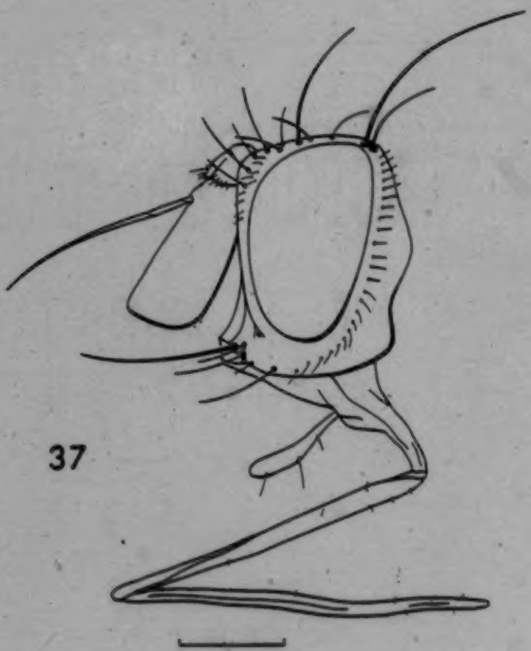

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Figs. 38-40. Male head profiles of *Siphona* species.

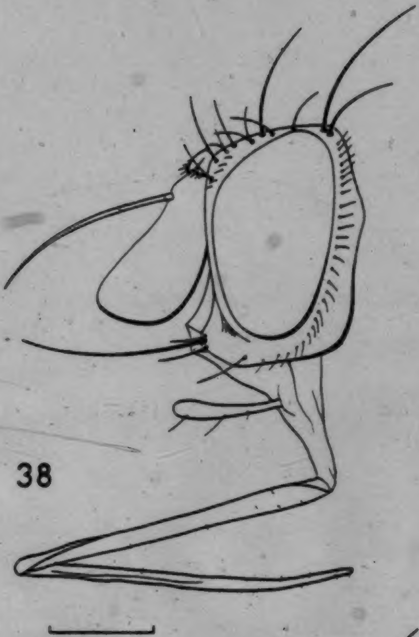
Fig. 38. *S. tropica*.

Fig. 39. *S. rizaba*.

Fig. 40. *S. unispina*.

Fig. 41. Head profile of female *S. lurida*.

Scale bars = 0.5mm.



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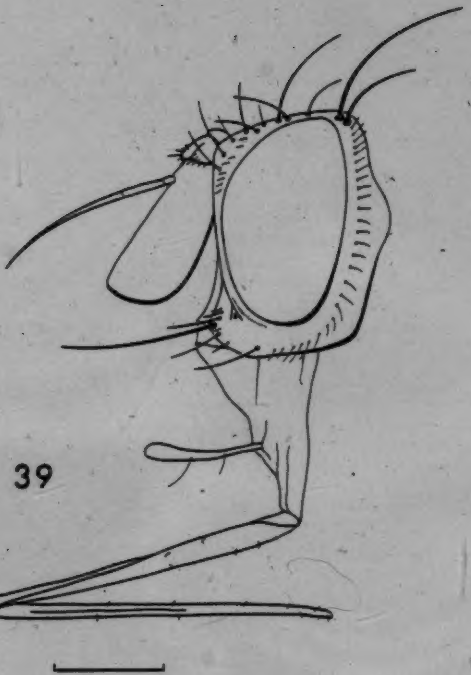

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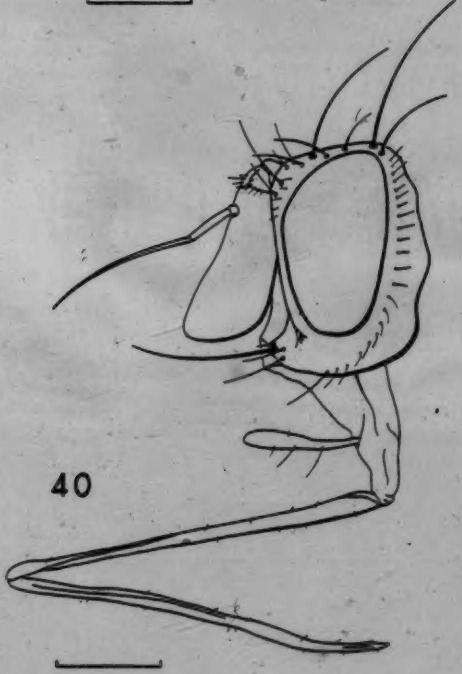

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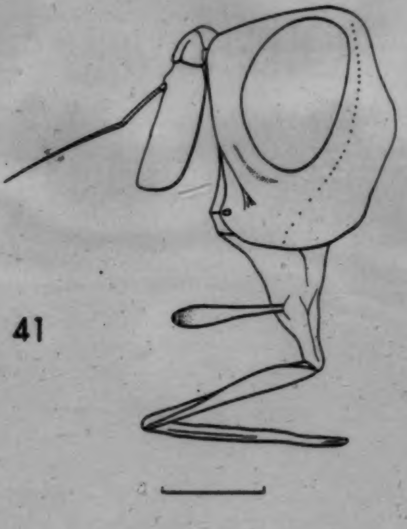

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Figs. 42-50. Female head profiles of *Siphona* species.

Fig. 42. *S. maculata*.

Fig. 43. *S. floridensis*.

Fig. 44. *S. intrudens*.

Fig. 45. *S. pacifica*.

Fig. 46. *S. cristata*.

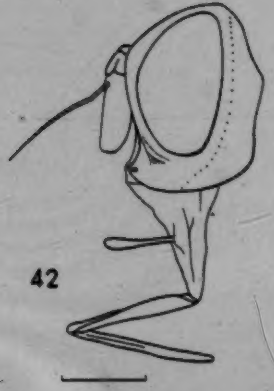
Fig. 47. *S. multifaria*.

Fig. 48. *S. lutea*.

Fig. 49. *S. pisinnia*.

Fig. 50. *S. geniculata*.

Scale bars = 0.5mm.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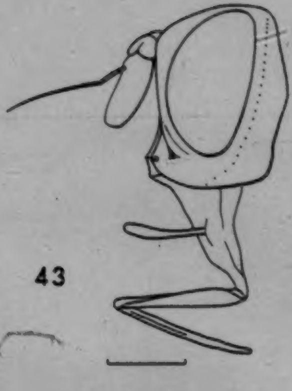
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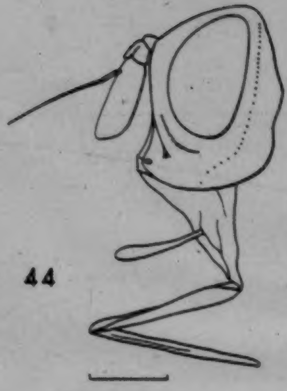
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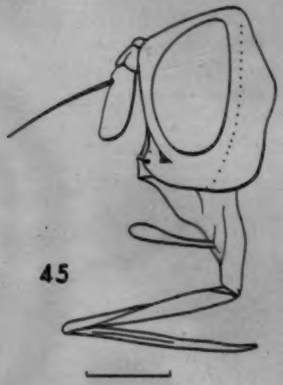
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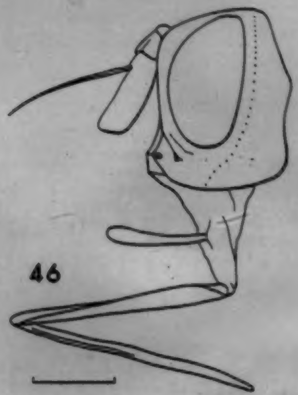
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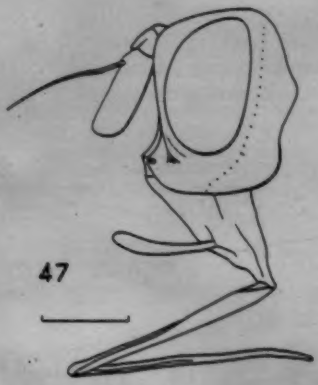
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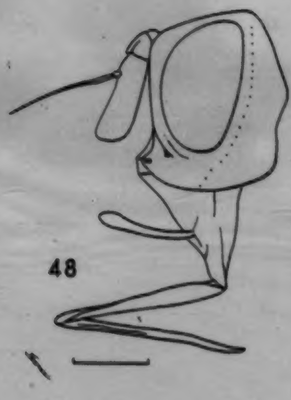
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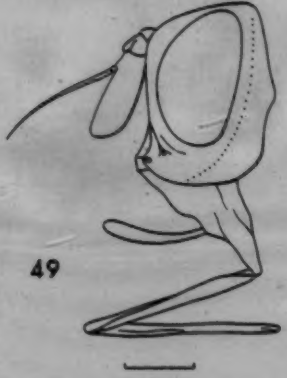
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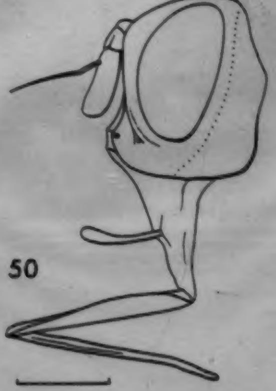
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Figs. 51-59. Female head profiles of *Siphona* species.

Fig. 51. *S. hokkaidensis.*

Fig. 52. *S. medialis.*

Fig. 53. *S. futilis.*

Fig. 54. *S. illinoiensis.*

Fig. 55. *S. brunnea.*

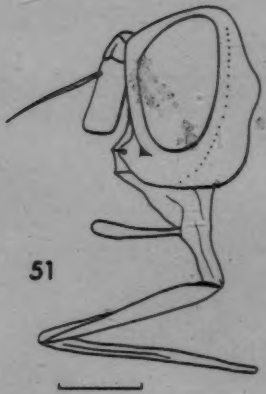
Fig. 56. *S. macronyx.*

Fig. 57. *S. tropica.*

Fig. 58. *S. rizaba.*

Fig. 59. *S. akidnomyia.*

Scale bars = 0.5mm.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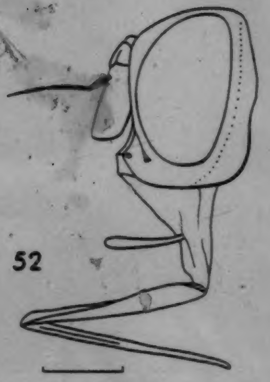
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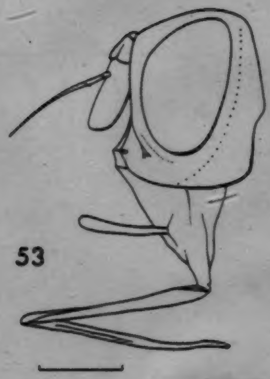
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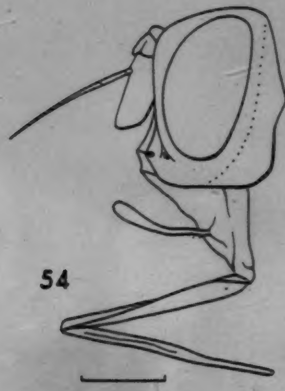
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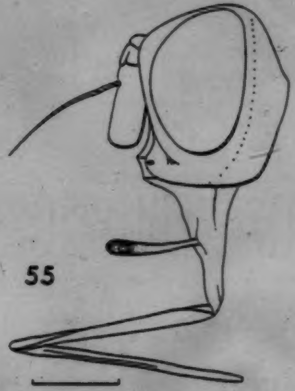
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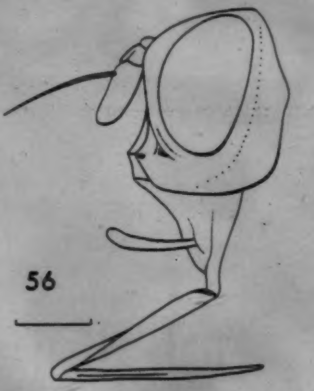
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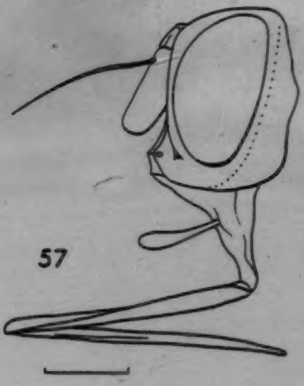
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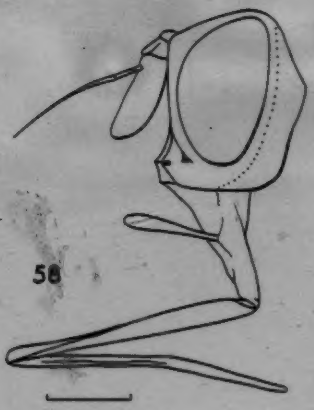
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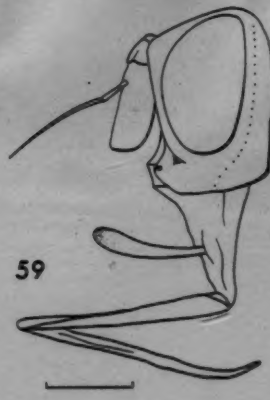
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Figs. 60-65. Male genitalia of *Siphona* species.

a. Anterior view of distiphallus.

b. Lateral view of genitalia.

Fig. 60. S. *maculata*.

Fig. 61. S. *floridensis*.

Fig. 62. S. *intrudens*.

Fig. 63. S. *lurida*.

Fig. 64. S. *pacifica*.

Fig. 65. S. *pisinnia*.

Scale bars = 0.1mm.

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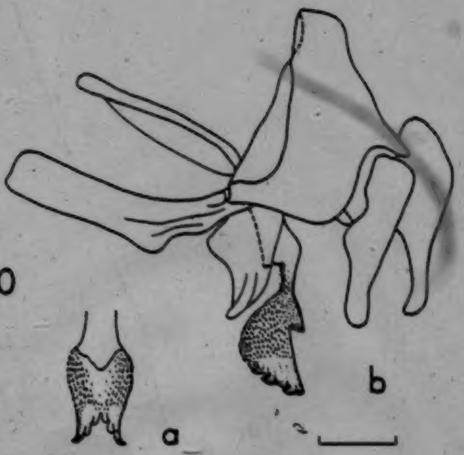

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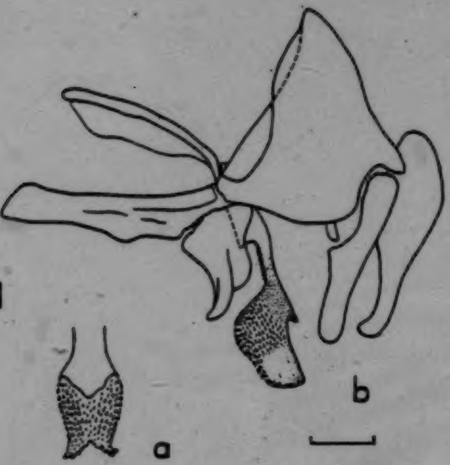

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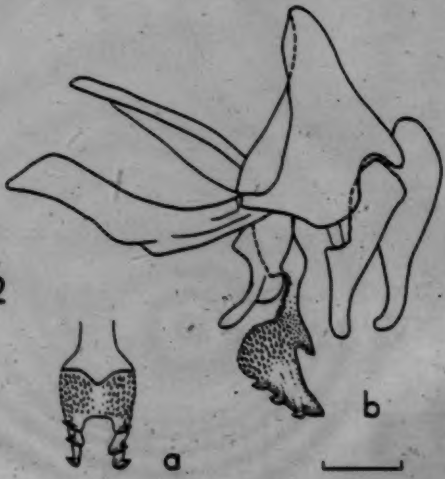

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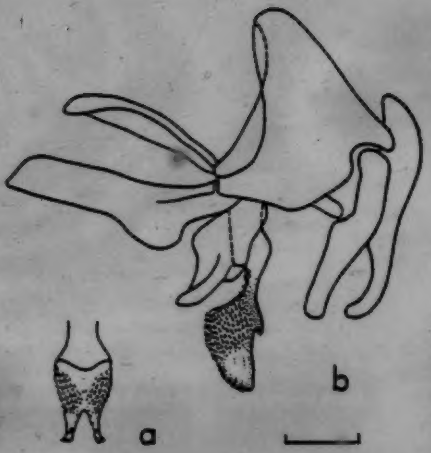

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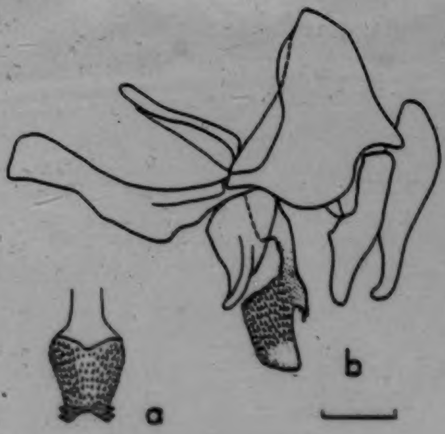

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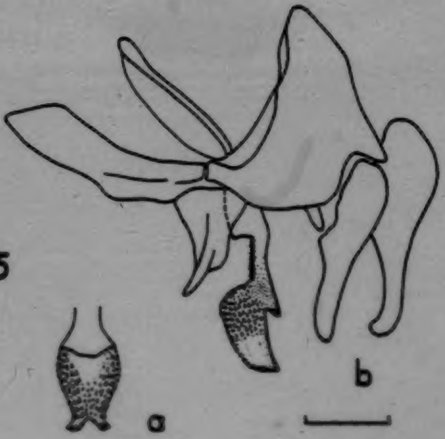


Figs. 66-71. Male genitalia of *Siphona* species.

a. Anterior view of distiphallus.

b. Lateral view of genitalia.

c. Lateral view of second distiphallus.

Fig. 66. *S. cristata*.

Fig. 67. *S. multifaria*.

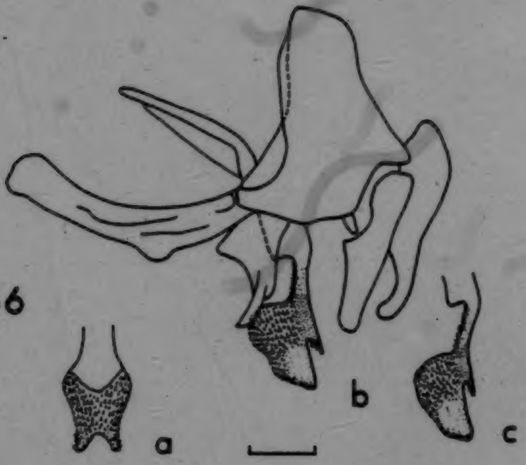
Fig. 68. *S. lutea*.

Fig. 69. *S. oligomyia*.

Fig. 70. *S. geniculata*.

Fig. 71. *S. hokkaidensis*.

Scale bars = 0.1mm.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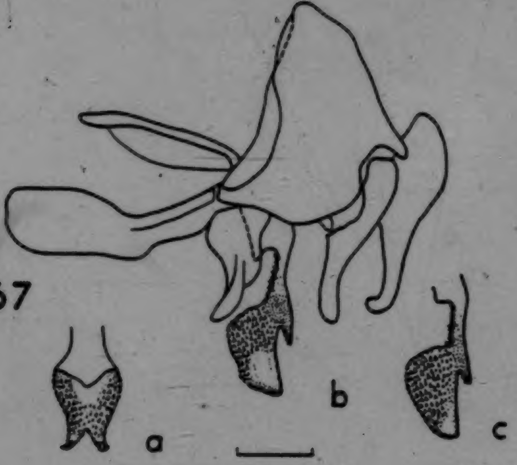
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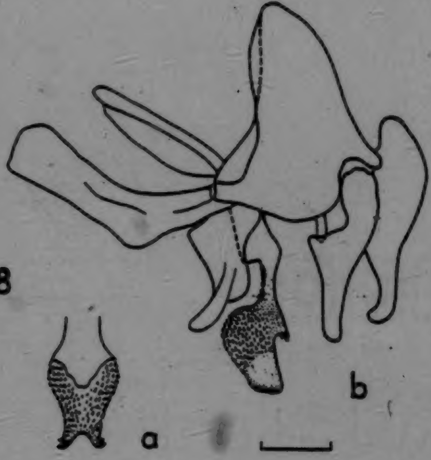
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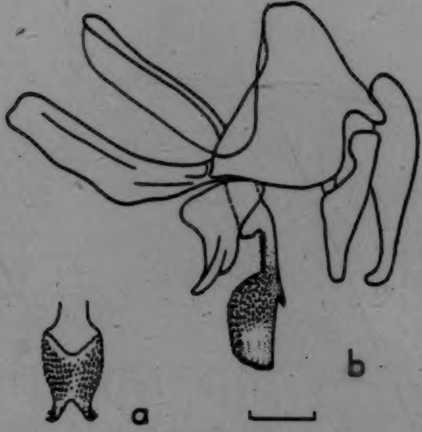
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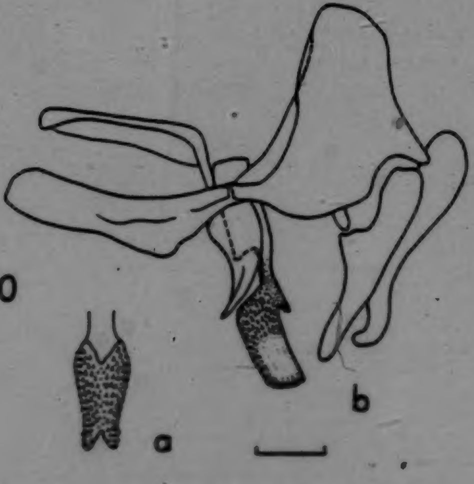
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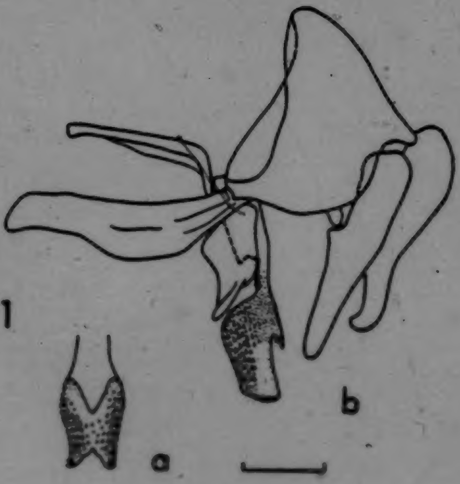
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Figs. 72-77. Male genitalia of *Siphona* species.

a. Anterior view of distiphallus.

b. Lateral view of genitalia.

Fig. 72. *S. medialis*.

Fig. 73. *S. futilis*.

Fig. 74. *S. brunnea*.

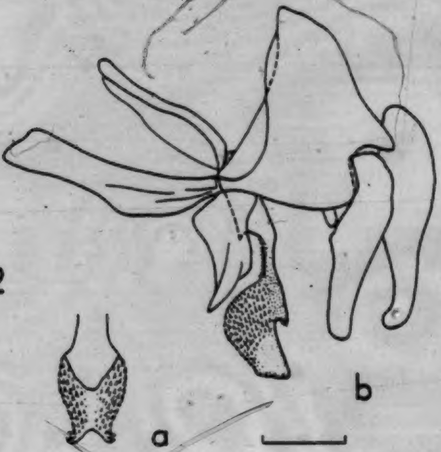
Fig. 75. *S. macronyx*.

Fig. 76. *S. akidnomyia*.

Fig. 77. *S. longissima*.

Scale bars = 0.1mm.

72



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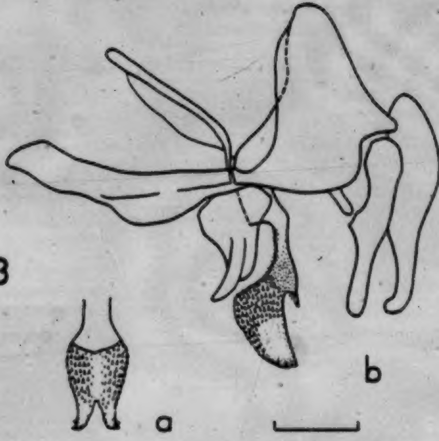

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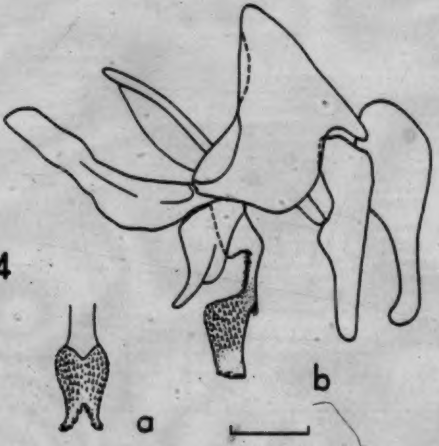

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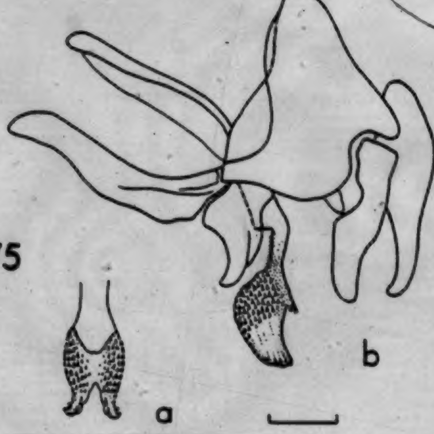

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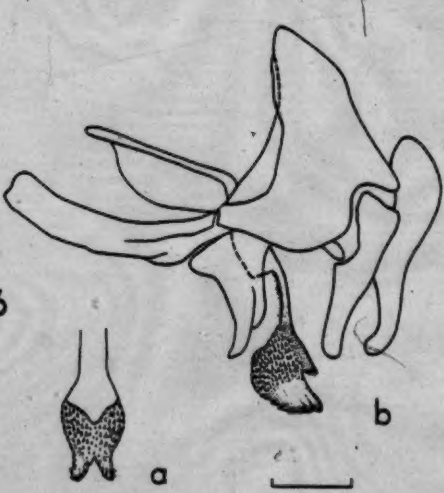

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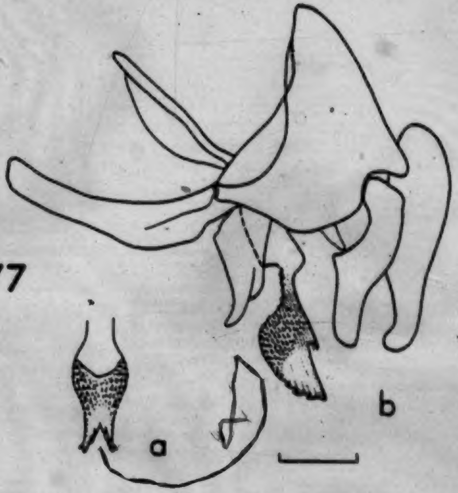


Figs. 78-80. Male genitalia of *Siphona* species.

a. Anterior view of distiphallus.

b. Lateral view of genitalia.

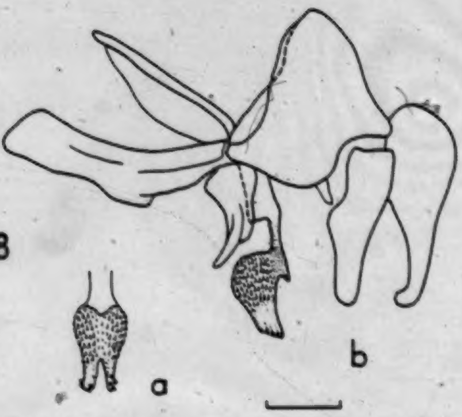
Fig. 78. *S. tropica*.

Fig. 79. *S. rizaba*.

Fig. 80. *S. unispina*.

Scale bars = 0.1mm.

78



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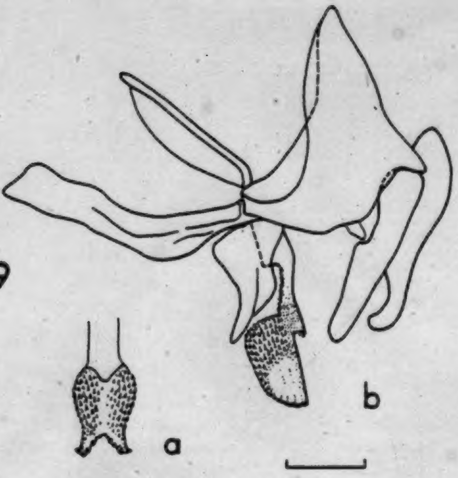


80

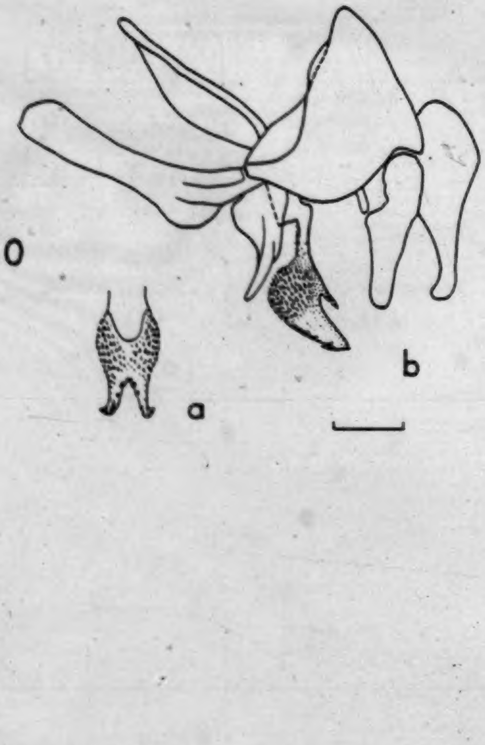
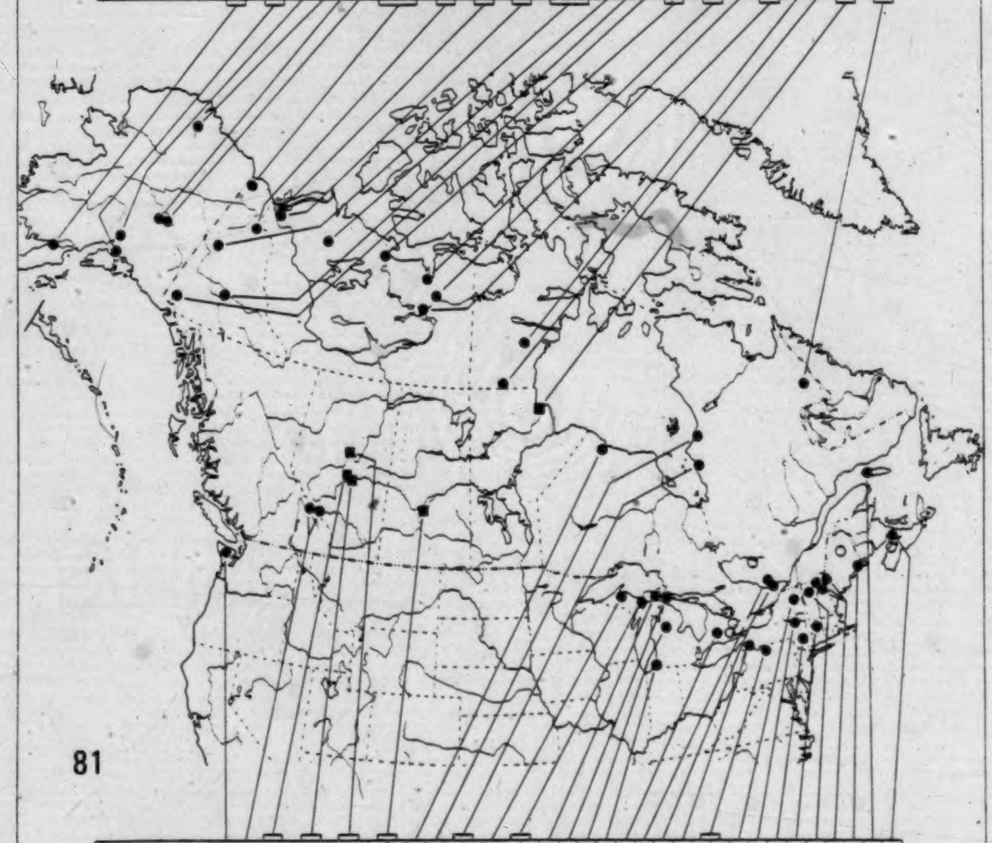


Fig. 81. Known North American distribution of Holarctic species *Siphona hokkaidensis*, with data on antennal type and abdominal setae. Dots denote locality records for *S. hokkaidensis* "b" (Figs. 13-16), and female specimens for which there were no male associates. Squares denote locality records for male specimens with antennal type 1, and associated females, from Alberta, Saskatchewan and Manitoba (*S. hokkaidensis* "a"). Rings signify locality records for which data were lacking.

Abbreviations: Antennal type 1, Fig. 30; type 2, Fig. 31; type 3, Fig. 32; f, female, Fig. 51. N, number of specimens in sample. No. of med. marg. on T_{1+2}, number of specimens with 0, 1 or 2 median marginal setae on T_{1+2}: 0, setae absent; 1, one seta on one side only; 2, 1 pair of setae. >1 pr. lat. marg. T_3, number of specimens with more than 1 lateral marginal seta on at least one side on T_3.

Antennal type		1	f	2	f	2	f	f	3	1	3	f	2	f	3	f	2	f	2	3	f	3	f	3	3	f	3	f	3	3	f	3	3	1	f	3	f
N		1	2	2	1	2	2	1	1	6	10	25	1	1	2	2	3	2	27	12	20	3	1	1	2	1	1	4	2	7	6	1	1	28	9	3	4
No. of med. marg. on T_{1+2}	2						2			5	9	15			2	2			1	4	1				2	1	1	1	1	3	3	1					2
	1									1	1	6							2	3	1	2						1	1	3			1	1		1	
	0	1	2	2	1	2		1	1			4	1	1			3	2	24	5	18	1	1	1				2		1	3			25	9	2	2
>1 pr. lat. marg. T_3							2			5	10	21		1	2	1			8	4	6	2		1	2	1	1	4	2	6	4	1	1	5		1	



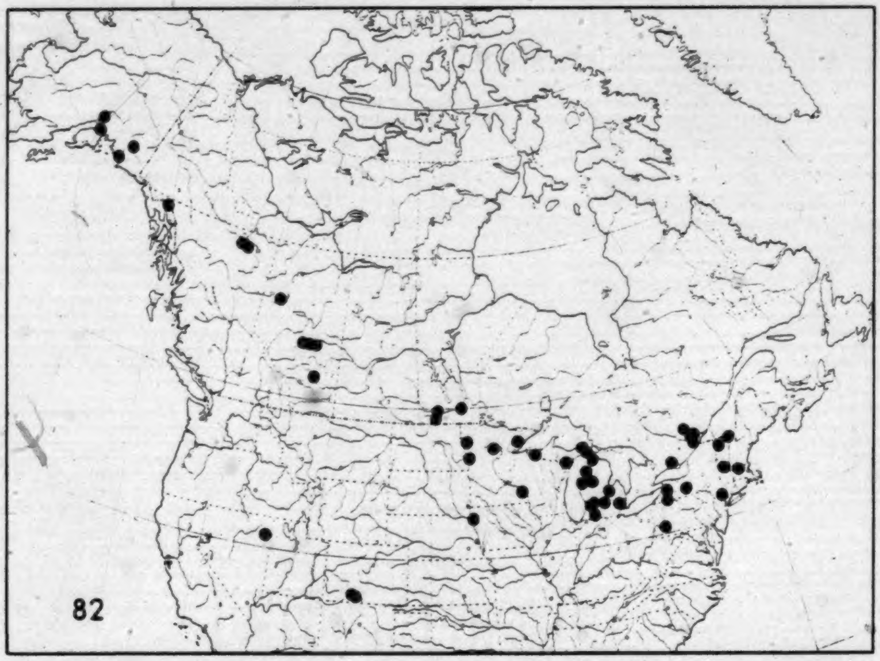
81

Antennal type		3	f	1	f	1	f	1	f	1	f	2	f	2	f	f	2	f	f	2	2	2	2	f	2	f	2	f	f	f	2	2	f	2	f	f	2
N		2	2	3	4	3	3	4	6	1	1	1	2	3	2	2	3	2	2	1	1	1	1	3	3	1	2	2	4	1	1	1	1	3	2	1	1
No. of med. marg. on T_{1+2}	2				2																																
	1		1		1				2				1												1				1								
	0	2	1	3	1	3	3	4	4	1	1	1	1	3	2	2	3	2	2	1	1	1	1	3	2	1	2	2	3	1	1	1	1	3	2	1	1
>1 pr. lat. marg. T_3		1							1					1	1												1	2		1				1	1		

Fig. 82. Known North American distribution of the Holarctic species *Siphona maculata* Staeger.

Fig. 83. Known distribution of *Siphona pisinnia* n. sp.

Fig. 84. Known distribution of *Siphona floridensis* n. sp.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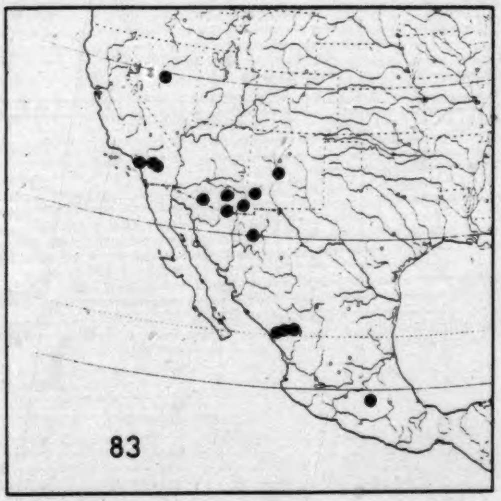

83

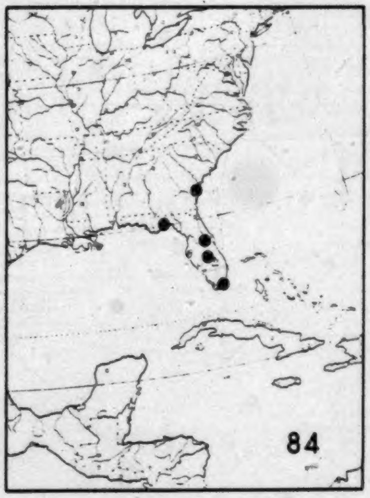
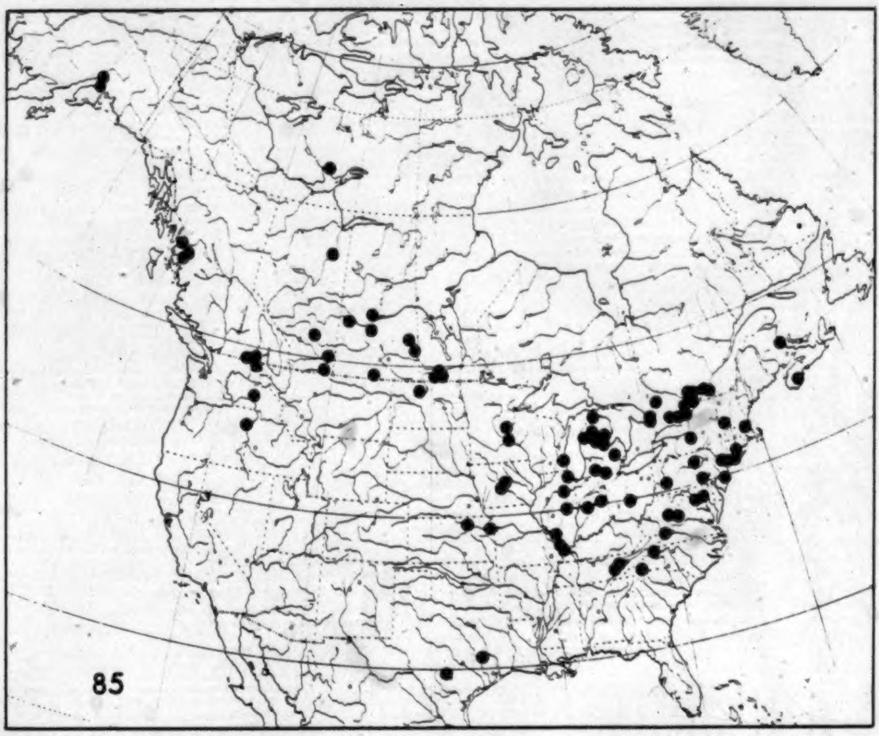

84

Fig. 85. Known distribution of *Siphona intrudens* (Curran).

Fig. 86. Known North American distribution of the Holarctic species *Siphona lurida* Reinhard.

Fig. 87. Known distribution of *Siphona pacifica* n. sp.

Fig. 88. Known distribution of *Siphona macronyx* n. sp.



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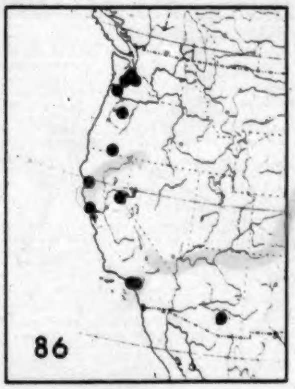
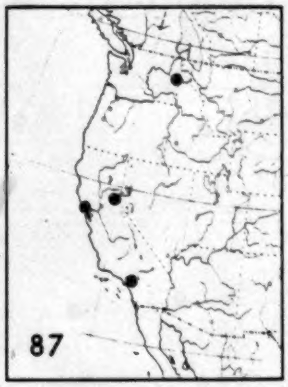
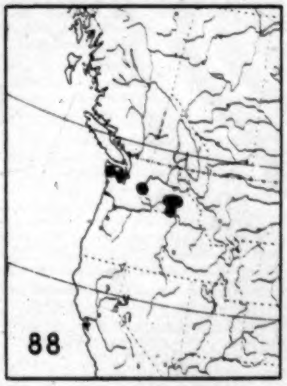


86



87



88

Fig. 89. Known distribution of *Siphona lutea* (Townsend).

Fig. 90. Known distribution of *Siphona oligomyia* n. sp.

Fig. 91. Known North American distribution of *S. geniculata* (De Geer) (introduced from the Palearctic Region).

Fig. 92. Known distribution of *Siphona illinoiensis* Townsend.

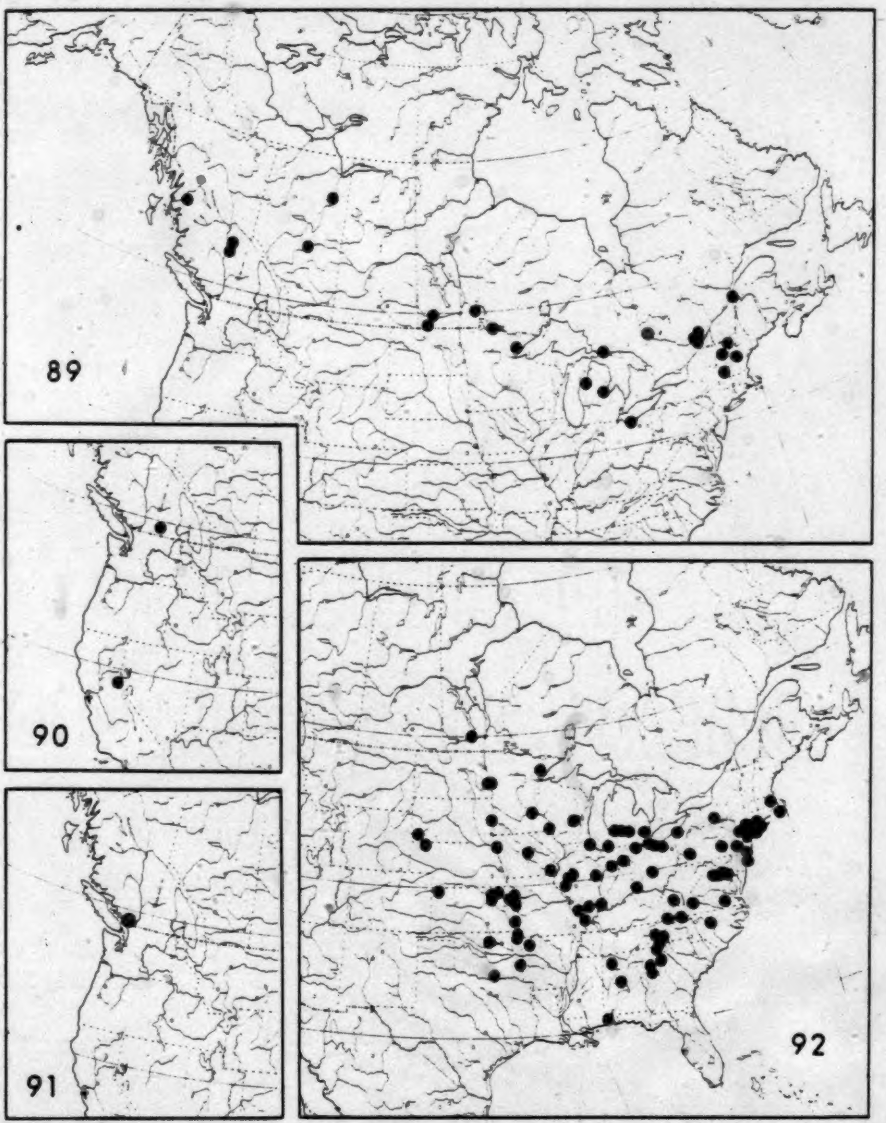

89
90
91
92

Fig. 93. Known distribution of *Siphona multifaria* n. sp.

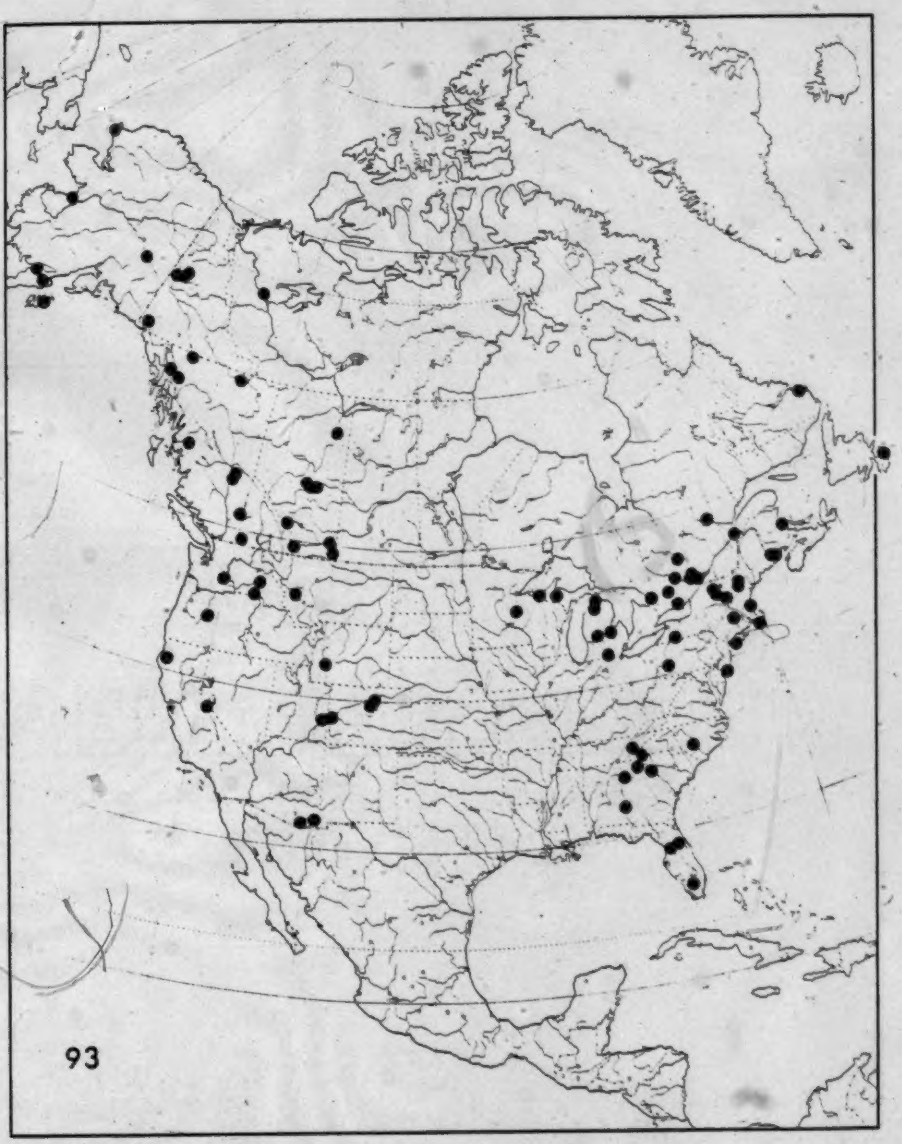
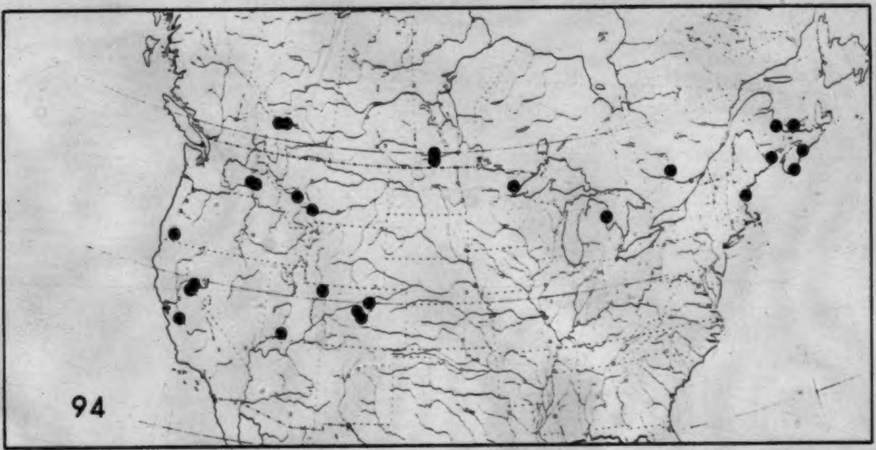
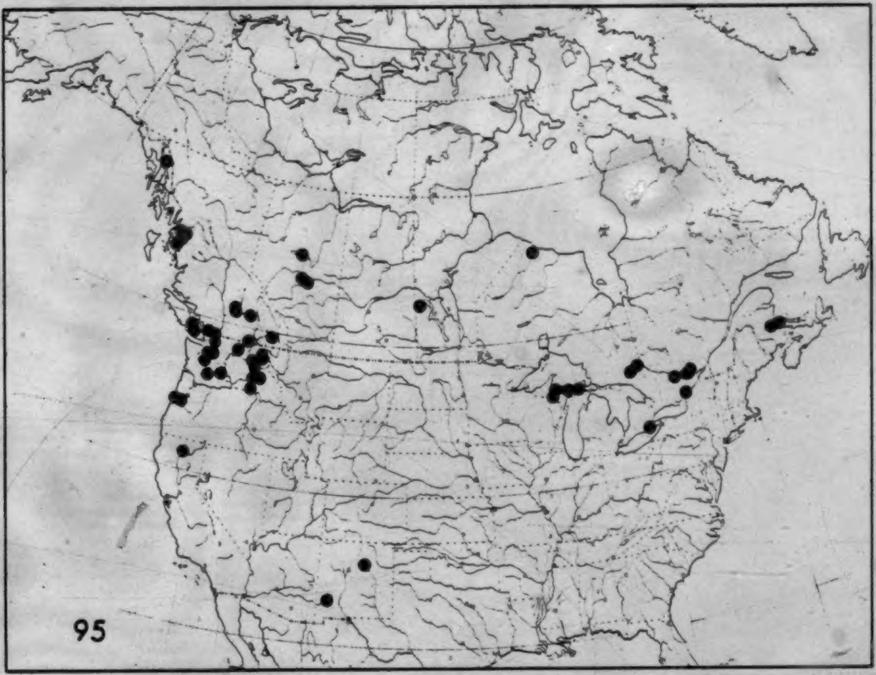

93

Fig. 94. Known distribution of *Siphona medialis* n. sp.

Fig. 95. Known North American distribution of the Holarctic species *Siphona cristata* (Fabricius).



94



95

Figs. 96-101. Known distributions of *Siphona* species.

Fig. 96. *Siphona futilis* van der Wulp.

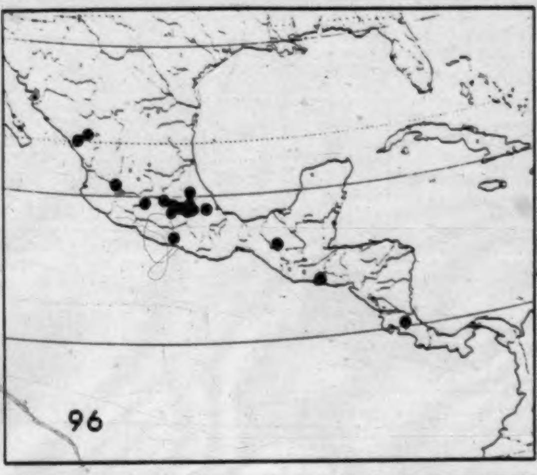
Fig. 97. *Siphona brunnea* n. sp.

Fig. 98. *Siphona rizaba* n. sp.

Fig. 99. *Siphona akidnomyia* n. sp.

Fig. 100. *Siphona longissima* n. sp.

Fig. 101. *Siphona tropica* (Townsend).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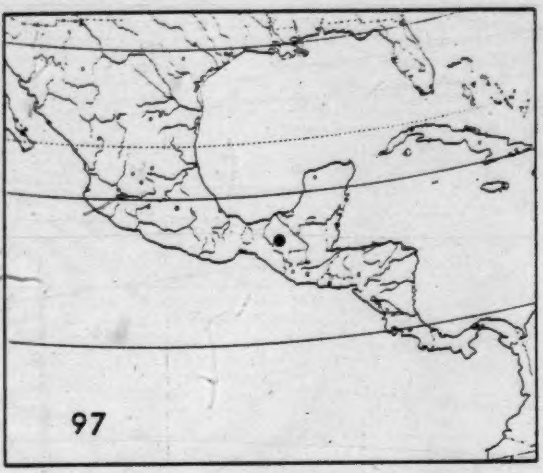
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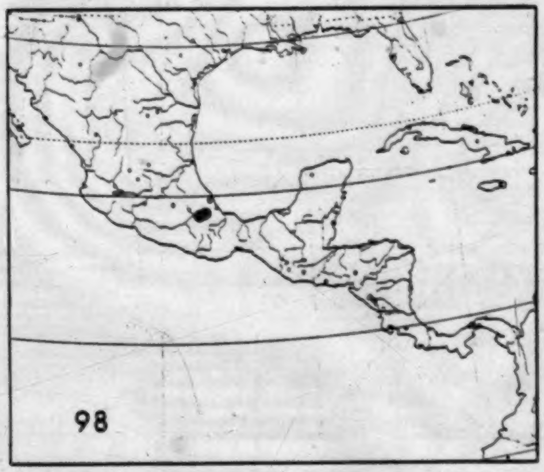
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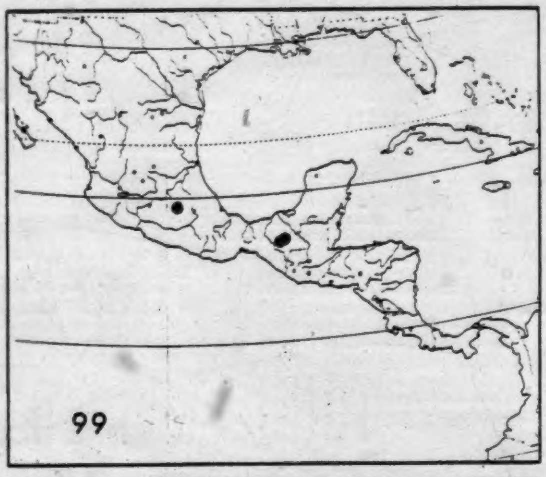
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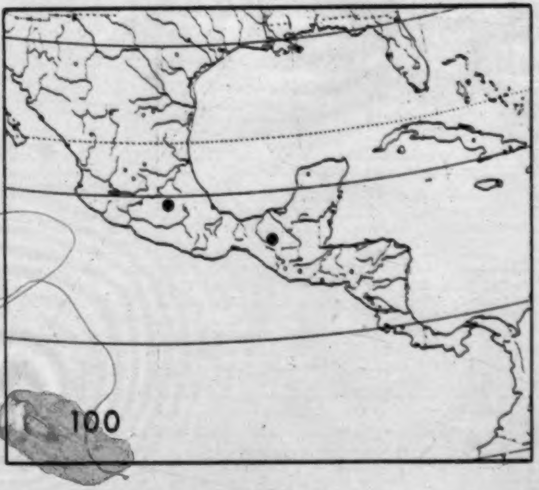

100

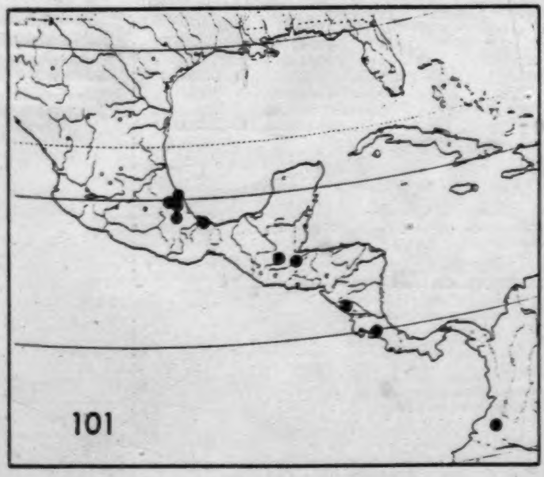
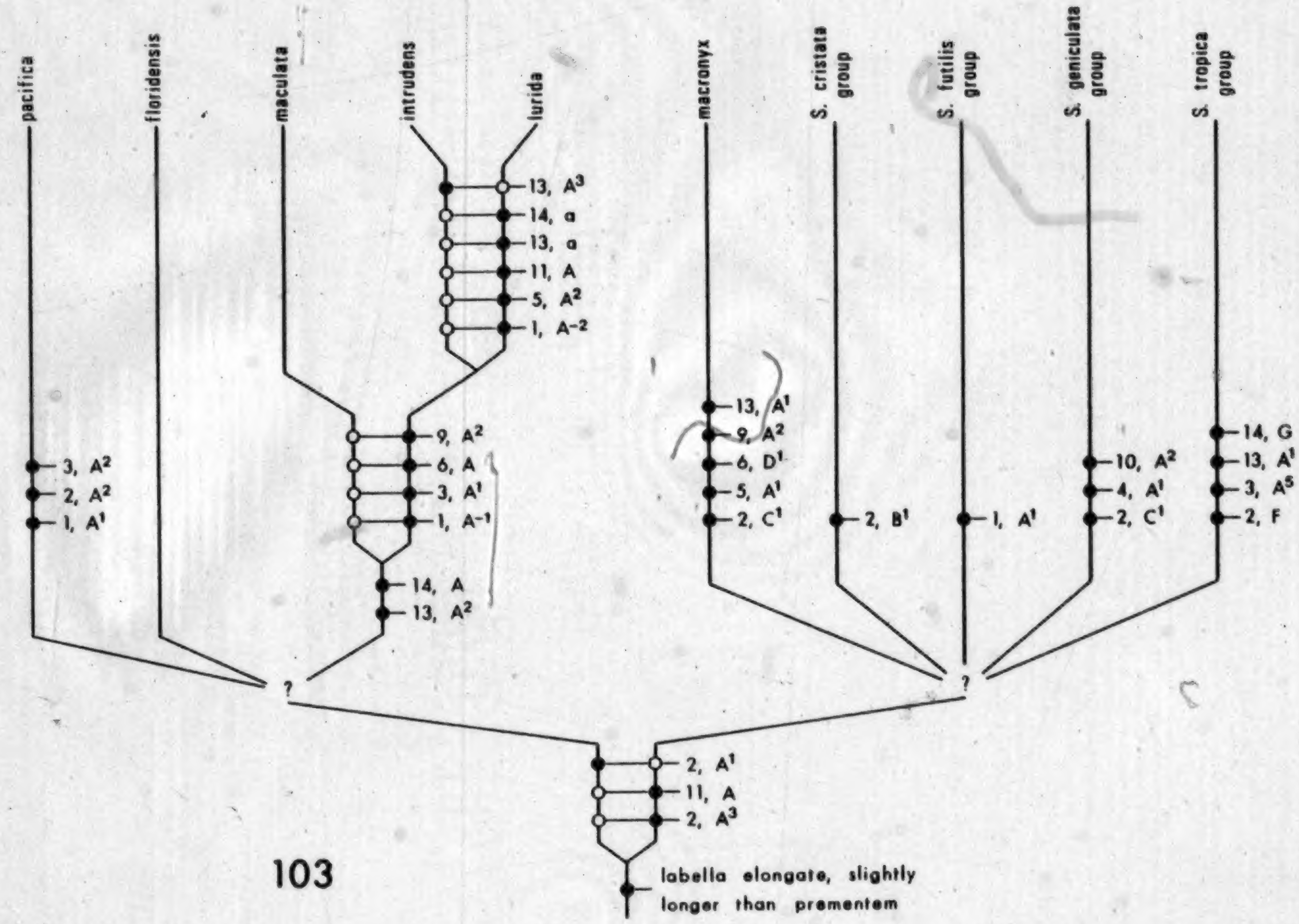

101

Fig. 102. Character matrix presenting the distribution of character states among North American *Siphona* species and African species *S. unispina* (Mesnil). Characters and states are discussed in "Phylogenetic interpretation" section.

Character Siphona species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
	Eye	Flagellomere 1	Proboscis	Aristomere 3	Vibrissal angle	Colouration	Wing setulae R_1	Wing setulae R_{4+5}	Tarsal claws	Median marginals	Lateral marginals	Sternum 5	Dentition on distiphallus	Distiphallus	Surstylus	No. of apotypies
maculata	a	A^1	a	a	a	a	a	a	a	a	a	a	A^2	A	a	3
floridensis	a	A^1	a	a	a	a	a	a	a	a	a	a	a	a	a	1
intrudens	A^{-1}	A^1	A^1	a	a	A	a	a	A^2	a	a	a	A^3	A	a	7
lurida	A^{-2}	A^1	A^1	a	A^2	A	a	a	A^2	a	A	a	a	a	a	7
pacifica	A^1	A^2	A^2	a	a	a	a	a	a	a	a	a	a	a	a	3
cristata	a	B^1	A^4	a	a	B^1	a	a	a	a	A	a	a	B	a	5
multifaria	a	B^1	A^4	a	a	a	a	a	a	a	A	a	a	B	a	4
lutea	a	B^1	A^2	a	a	B^2	A	A	a	a	A	a	a	B	a	7
oligomyia	A^{-1}	A	A^3	a	a	B^2	A	a	A^1	a	A	A	a	a	a	8
pisinnia	a	B^2	A^3	a	a	a	a	a	a	a	A	a	a	a	a	3
geniculata	a	C^1	A^3	A^1	a	a	a	a	A^1	A^2	B	a	a	C	A	8
hokkaidensis	a	D	A^3	A^2	a	a	a	a	a	A^1	B	a	a	C	A	7
medialis	A^2	C^1	A^3	A^1	a	C	a	a	a	A^2	A	a	a	a	a	7
futilis	A^2	C^1	A^3	a	a	a	a	a	a	a	A	a	a	D	a	5
illinoiensis	A^2	C^2	A^3	a	a	a	a	a	a	a	A	a	a	D	a	5
brunnea	A^1	E	A^3	a	a	D^2	a	a	A^1	a	A	a	a	E	a	7
tropica	A^2	F	A^5	a	a	a	A	a	a	a	A	a	a	G	a	6
rizaba	A^2	F	A^5	a	a	a	a	a	a	a	A	a	a	a	A	5
longissima	A^1	F	A^5	a	a	a	a	a	A^1	a	A	a	A^1	G	a	7
akidnomyia	a	F	A^4	a	a	a	a	a	A^2	a	A	a	A^1	F	a	6
unispina	a	F	A^5	a	a	a	A	A	a	a	A	a	A^1	G	a	7
macronyx	a	C^1	A^3	a	A^1	D^1	a	a	A^2	a	A	a	A^1	a	a	7

Fig. 103. Cladogram illustrating inferred relationship between the *S. maculata* group and the other North American *Siphona* species groups, with a hypothetical phylogeny of North American species of the *S. maculata* species group. Dots denote apotypic character states, rings plesiotypic states. For explanation and discussion of characters and states see Fig. 102 and "Phylogenetic interpretation" section.


pacifica
3, A^2
2, A^2
1, A^1
floridensis
maculata
intrudens
lurida
13, A^3
14, a
13, a
11, A
5, A^2
1, A^{-2}
9, A^2
6, A
3, A^1
1, A^{-1}
14, A
13, A^2
macronyx
13, A^1
9, A^2
6, D^1
5, A^1
2, C^1
S. cristata group
2, B^1
S. futilis group
1, A^1
S. geniculata group
10, A^2
4, A^1
2, C^1
S. tropica group
14, G
13, A^1
3, A^5
2, F
?
?
2, A^1
11, A
2, A^3
labella elongate, slightly longer than prementem

103

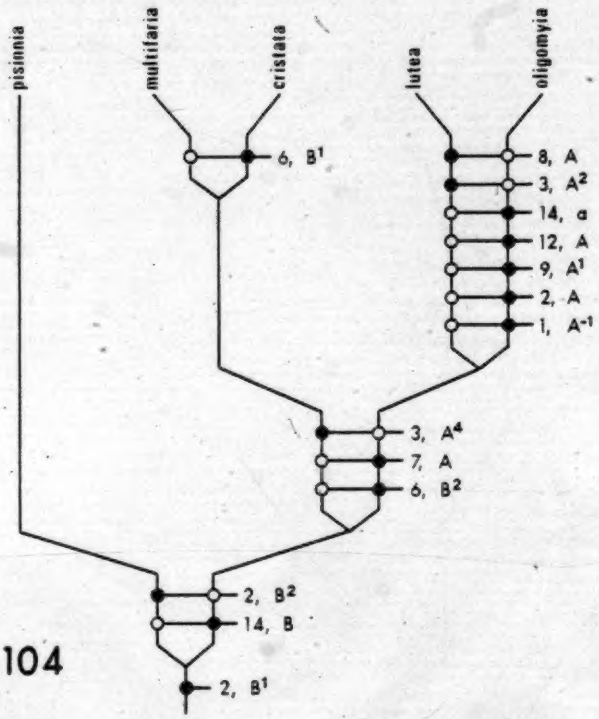
Figs. 104-107. Cladograms illustrating hypothetical phylogenetic relationships among North American species of *Siphona* species groups. Dots denote apotypic character states, rings plesiotypic states. For explanation and discussion of characters and states see Fig. 102 and "Phylogenetic interpretation" section.

Fig. 104. The *S. cristata* group.

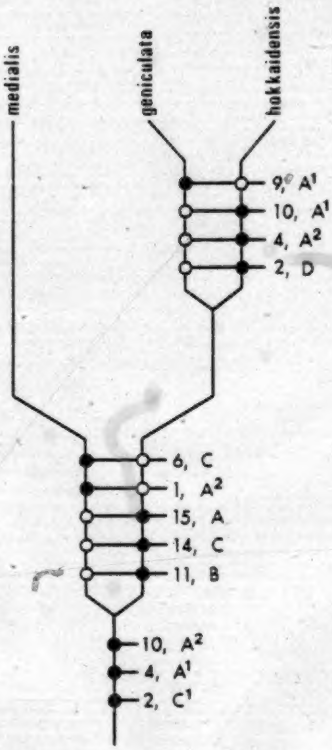
Fig. 105. The *S. geniculata* group.

Fig. 106. The *S. tropica* group.

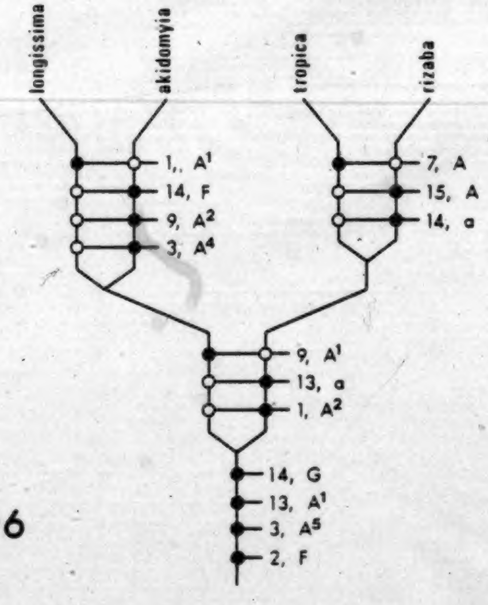
Fig. 107. The *S. futilis* group.


pisinnia
multifaria
cristata
lutea
oligomyia
6, B^1
8, A
3, A^2
14, a
12, A
9, A^1
2, A
1, A^{-1}
3, A^4
7, A
6, B^2
2, B^2
14, B
2, B^1

104


medialis
geniculata
hokkaidensis
9, A^1
10, A^1
4, A^2
2, D
6, C
1, A^2
15, A
14, C
11, B
10, A^2
4, A^1
2, C^1

105


longissima
akidomyia
tropica
rizaba
1,. A^1
14, F
9, A^2
3, A^4
7, A
15, A
14, a
9, A^1
13, a
1, A^2
14, G
13, A^1
3, A^5
2, F

106

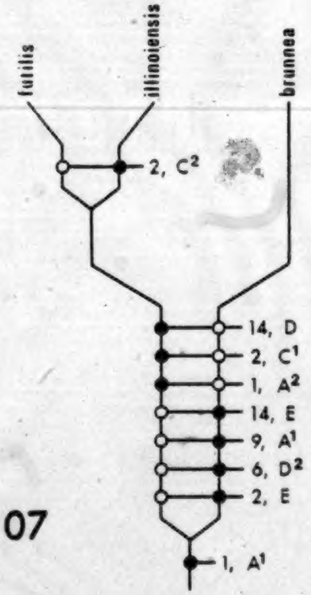

futilis
illinoiensis
brunnea
2, C^2
14, D
2, C^1
1, A^2
14, E
9, A^1
6, D^2
2, E
1, A^1

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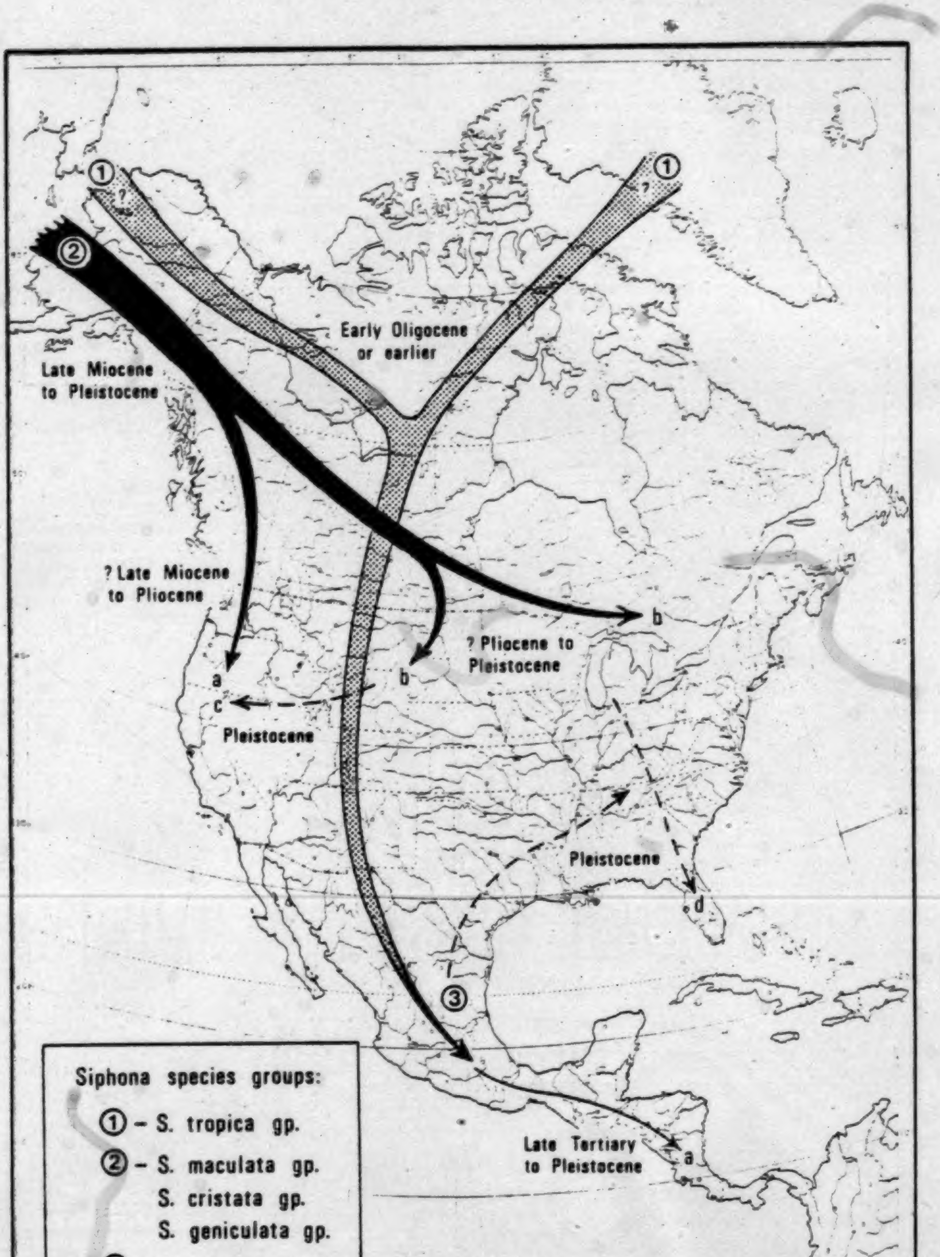
Fig. 108. Generalized historical zoogeography of North American species of *Siphona*, as inferred from a cladistic analysis and species distributions.

(1) *S. tropica* group - migration into North America through Beringia or across a North Atlantic land bridge prior to Early Oligocene during Tertiary climatic optimum, with subsequent diversification in Mexico. (a) Late Tertiary to Pleistocene migration of taxa into Central and South America.

(2) *S. maculata*, *S. cristata* and *S. geniculata* groups - first representatives arrived in North America since Late Miocene; exchange continued into Pleistocene. (a) Oldest taxa of these groups might have become associated with the developing Rocky Mountain biota (?Late Miocene - Pliocene). (b) Transcontinental, cool to cold temperate taxa, indicative of later invasions (?Pliocene --Pleistocene). (c) Vicariance of *S. lutea* and *S. oligomyia* (Pleistocene). (d) Vicariance of *S. maculata* and *S. floridensis* (Pleistocene).

(3) *S. futilis* group - place and age of origin uncertain. Vicariance of *S. futilis* and *S. illinoiensis* (Pleistocene).


①
①
②
Early Oligocene
or earlier
Late Miocene
to Pleistocene
? Late Miocene
to Pliocene
? Pliocene to
Pleistocene
a
c
b
b
Pleistocene
Pleistocene
d
③
Late Tertiary
to Pleistocene
a
Siphona species groups:
① – S. tropica gp.
② – S. maculata gp.
S. cristata gp.
S. geniculata gp.
③ – S. futilis gp.

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